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## ERRATA

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- 23, line 22. *For latifolia read latifolius.*
- 37, line 11 from bottom. *For Schlechteri read Schlechteri.*
- 152, centre, right-hand column. *For Micrasterias truncata read Micrasterias crenata.*
- 152, line 18 from bottom, right-hand column. *For Cosmarium Hammeri var. homolodermum read Cosmarium Hammeri var. homalodermum.*
- 152, line 15 from bottom, right-hand column. *For Cosmarium Novae-Semliae var. sibiricum read Cosmarium Novae-Semliae var. sibiricum.*
- 152, line 11 from bottom, right-hand column. *For Cosmarium speciosum f. trigona read Cosmarium speciosum f. triquetra.*
- 316, column 3. *For H. humifumus read H. humifusum.*
- 424, line 10. *For undecorated read undecorticated.*
- 425, line 8 from bottom. *For wth read with.*

## EXPLANATION OF THE PLATES

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### PLATE

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- 5. Development of the wheat plant.
- 6-7. *Saxifraga Geum* and *Saxifraga punctata*.
- 8-10. *Pariana* spp.
- 11-13. *Elettaria Cardamomum* Maton.
- 14-20. Aquatic Phycomycetes.
- 21-22. *Potamogeton Schweinfurthii*.
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A revision of the South African species of *Juncus*. By Professor R. S. ADAMSON, M.A., D.Sc. (Communicated by the Botanical Secretary)

[Read 1 March 1934]

AN investigation of the species of *Juncus* found on the Cape Peninsula was subsequently extended to include those of the whole of the Union of South Africa. In an area of this size it is obvious that collection and examination of plants over large areas must be very incomplete and knowledge of distribution very unequal.

It was found that much of the material in herbaria was named with considerable uncertainty and, further, several plants were discovered which could not be assigned to any of the existing species. Again, the limits of species seemed uncertain, and either overlapped or were so wide as to include plants certainly different.

In the present investigation the plants have been studied, as far as was possible, in the living state in the field, and the results so accumulated compared and correlated with material in herbaria. In addition to the older collections, some more recent have been studied, especially those of the late Professor C. E. Moss, which have proved invaluable. Further, through the kindness of Mrs. Moss, I have had access to a number of his MS. notes, of which I have made full use.

In the course of the work I have examined the material in the following herbaria :—British Museum (Natural History), London ; Royal Botanic Gardens, Kew ; Botany School, Cambridge ; Botanical Museum, Stockholm ; Botanische Garten, Berlin-Dahlem ; Bolus Herbarium, Cape Town ; South

African Museum, Cape Town ; Guthrie Herbarium, University of Cape Town ; National Herbarium, Pretoria ; Albany Museum, Grahamstown ; Veterinary Department, Onderstepoort ; University of the Witwatersrand, Johannesburg ; University of Stellenbosch.

I have to express my thanks to the directors and the curators of these institutions for allowing free access to the collections, and in many cases for permitting the borrowing of material for study. I have especially to thank Mr. J. Ramsbottom, Keeper of Botany, British Museum, for obtaining on loan the sheets from the collections in Berlin and in Stockholm for examination in London.

The South African species of the cosmopolitan genus *Juncus* were monographed by Fr. Buchenau in 1875 ('Monographie der Juncaceen vom Cap', in *Abh. Nat. Ver. Brem.* iv, 393-512, t. v-xi). Buchenau then recognised twenty-nine species, of which ten were described for the first time. This work made a real advance in knowledge, and has been the basis of subsequent investigations. This account was incorporated with little alteration by Buchenau in his 'Monographia Juncacearum' in 1890 (in *Engler, Bot. Jahrb.* xii, 1), and was essentially unchanged in his account of the family in *Engler, 'Das Pflanzenreich'*, iv, 36 (1906). These three monographs by Buchenau are often referred to in the following pages and for brevity are quoted by their dates. The account by Baker in '*Flora Capensis*' (vii (1895) 17-27) is almost entirely based on Buchenau, though a few alterations were made ; *J. Kraussii* was sunk in *J. maritimus* and *J. bufonius* grouped with the annual species of Buchenau's '*Junci graminifolii*'.

In Buchenau's monographs the species are of somewhat unequal rank. Many treated as separate units are nearly allied, while others are certainly aggregates. This was perhaps inevitable with the rather limited herbarium material available at that time. These aggregate species are now rearranged—for example, *J. capensis* and *J. Dregeanus* as defined by Buchenau are subdivided into four and three species respectively. It is hoped that the resulting arrangement gives units more equal in rank and more natural in their limitations.

In this revision the number of species is raised to forty, of which eight are described as new. Four previously described as varieties or subspecies are raised to specific rank. Of those given by Buchenau three are reduced, two to varietal rank and one is sunk in another species. Two species not recorded by Buchenau are included.

In the subdivision of the genus the arrangement and nomenclature of Buchenau, which has received fairly general acceptance, has been adopted. Of the eight subgenera or series, one, '*Junci singulares*', is merged in the '*Junci graminifolii*'. Of the remainder, five are represented in the South African Flora: the '*Junci subulati*' and '*Junci alpini*' have no representatives in the Southern Hemisphere. Of those present the largest is '*Junci graminifolii*', which comprises twenty-five of the forty recognised species ;

'*J. septati*' contain six; '*J. thalassici*' four; '*J. poiophylli*' three; and '*J. genuini*' two. None of the three species in '*Junci poiophylli*' is an undoubted native of South Africa.

Of the forty species, twenty-seven are endemic to South Africa and four others are only recorded outside in the immediately adjacent countries. In other words, three quarters of the known species are wholly S. African in distribution. Of the endemics twenty-two belong to the *Junci graminifolii*.

Under each species a list of localities is given in which only specimens actually seen and examined are quoted. The distributions there given are patently incomplete. Further collecting and field work are necessary before any generalisations can be drawn from the geographical distribution of the species.

JUNCUS [Tournefort, Inst. rei Herb. i, p. 246 (1700); Linn. Syst. Nat. p. 6 (1735); et Gen. Pl. p. 104 (1737)]; Linn. Sp. Pl. p. 325 (1753); Benth. & Hook. Gen. Pl. iii. p. 867 (1880); Vierhapper, in Engler & Prantl, Nat. Pflanz. Auf. 2, 15 a, p. 214 (1930).

Glabrous annuals or perennials. Flowers with perianth of 6 free, glume-like or membranous tepals. Stamens 6, less often 3, hypogynous. Gynaecium of 3 carpels, fruit a capsule, with numerous seeds.

JUNCI POIOPHYLLI Buchen. in Abh. Nat. Ver. Brem. iv, p. 406 (1875); in Engler Bot. Jahrb. xii, p. 169 (1890); in Das Pflanzenr. iv, p. 36 (1906) 100. *Tenagaia* Dumort. (1827), *fide* T. v. Post & O. Kuntze, Lex. Gen. Phan. p. 303 (1904). *Isophyllum* Koch, in Linnaea, xxi, p. 628 (1848).

Flowers with prophylls (bracteoles). Leaves mostly basal, flat, channelled, or subterete. Inflorescence with separate flowers, not capitula. Annual or perennial.

#### Key to South African Species.

- |  |                            |
|--|----------------------------|
| 1. Annual, perianth with long green points exceeding capsule. . . . .                      | 1. <i>J. bufonius</i> .    |
| Perennial, inflorescence terminal or pseudolateral, leaves subterete . . . . .             | 2.                         |
| 2. Inflorescence terminal, flowers large, capsule brown, much exceeding perianth . . . . . | 2. <i>J. Chamissonis</i> . |
| Inflorescence, pseudolateral with long subtending leaf; flowers few, small, pale . . . . . | 3. <i>J. capillaceus</i> . |

1. JUNCUS BUFONIUS Linn. Sp. Pl. i, p. 328 (1753); Buchen. p. 175 (1890); p. 105 (1906); Baker, in Flora Cap. vii, p. 23 (1895). *J. ranarius* Nees, in Linnaea, xx, p. 243 (1847) (nomen).

Annual, tufted. Leaves slender, channelled above, equalling stems. Stems up to 20 cm. simple or forked. Flowers solitary or in groups of 2-6, 4-6 mm. long. Perianth with long green points, external longer. Capsule almost equalling inner perianth, oblong, shining, red-brown, obtuse, flattened at top, very shortly apiculate.

The commonest S. African form of this variable species has the flowers in

flattened groups of four to six, rarely eight, and a dark reddish capsule equalling the inner perianth. C. E. Moss (in MS.) identified this with *J. hybridus* Brot. Fl. Lusit. i, p. 513 (1804). The plants certainly agree very well with the description. But various transitions can be found between this common form and those with solitary flowers on an extended inflorescence which would be referred to *J. bufonius* var. *genuinus* Coutinho, Bot. Soc. Brot. viii, p. 102 (1890). Without culture and genetic experiments it seems inadvisable to create new species or varieties and so add to the already complicated synonymy of the forms included in this species.

*J. bufonius* occurs by roadsides and in disturbed ground. It is probably not an original native, but an established alien. It is generally distributed through the western and south-western Cape, but apparently is rare or absent in the east, and is less common in the interior.

CAPE PROVINCE :—NAMAQUALAND : Steinkopf, *Schlechter* 11481! Kariëboomfontein, *Pearson* 4988! CLANWILLIAM, *Leipoldt* 345! CERES : Ceres, *Pearson* 3252! *Pillans* 18429! PAARL : Berg River, *Zeyher* 4314! CAPE : Cape Town, *Ecklon* 4314! *Mey*! *Drège* 8790, p.pt.! *Burchell* 2132! Table Mt., *Moss* 5634! 7930! 7931! 7932! *Adamson* 10! 275! *Levy*! Kirstenbosch, *W. Dod* 2265! *Adamson* 236! Rondebosch, *Adamson* 201! 330! Claremont, *Schlechter* 1673, p.pt.! *W. Dod* 2132! Fishhoek, *Adamson* 259! *Levy*! Camps Bay, *Adamson* 8! 9! Cape Flats, *Moss* 4186! 5616! *Zeyher* 4968, p.pt.! *Adamson* 150! 216! 222! Milnerton, *Adamson* 13! STELLENBOSCH : Somerset West, *Zeyher* 83! Hottentots Holland, *Gueinzus*! Stellenbosch, *Duthie* 1713.1803! CALEDON : Onrust, *Adamson* 11! 12! PT. ELIZABETH : Walmer, *Paterson* 2379! UITENHAGE, *Paterson* 2354! 2379! LAINGSBURG : Buffels River, *Schlechter* 11253!

ORANGE FREE STATE :—Bloemfontein, *Potts* 2870!

UNLOCALISED :—*Schlechter* 5867! *Drège*, a! *Zeyher* 6! *Wallich & Hartman*!

2. *JUNCUS CHAMISSONIS* Kunth, Enum. Pl. iii, p. 348 (1841); Buchen. p. 198 (1890); *Adamson*, in S. Afr. Journ. Sci. xxviii, p. 251 (1931). *J. imbricatus* var. *Chamissonis* Buchen. p. 122 (1906).

Tufted, rhizome rather deep, branched. *Stems* tough, up to 50 cm. finely striated. *Sheaths* 2–3, bearing semiterete, grooved blades, about half length of stem. *Inflorescence* terminal, subtending leaf equalling or exceeding inflorescence, branches ascending. *Flowers* solitary, regularly spaced on upper side of branches, 5–8 mm. long. *Bracts* bright chestnut-colour, shorter than flowers. *Perianth* equal, hard, brown, with green midrib. *Stamens* 6, shorter than perianth. *Style* very short. *Capsule* much exceeding perianth, round-pyramidal, shining olive-brown. *Seeds* very shortly apiculate.

A S. American species naturalised, and spreading, in the neighbourhood of Cape Town.

CAPE PROVINCE :—CAPE : Rondebosch (Camp Ground), *Levy's*! (Keurboom Park), *Adamson* 338! Kirstenbosch, *Compton*! *Adamson* 4! 7! Rose bank, *Adamson* 336! 337! Cape Flats (Lansdowne), *Adamson* 221!

3. *JUNCUS CAPILLACEUS* Lam. Enc. Meth. Bot. iii, p. 267 (1789); Kunth, Enum. Pl. iii, p. 350 (1840); Buchen. p. 199 (1890), p. 122 (1906); *Adamson*, in S. Afr. Journ. Sci. xxviii, p. 251 (1931).

Tufted, rhizomes straight, not branched. Shoots to 25 cm., slender, soft. Sheaths 1, rarely 2, with subterete, slightly grooved blades. Leaves equalling stems. Inflorescence pseudolateral, small, 2–10 fld. Flowers stalked, 3–4 mm., pale. Perianth equal. Stamens 6, shorter than perianth. Capsule pale, exceeding perianth, retuse, bluntly 3-angled. Seeds small, brown.

A South American species established on roadsides near Cape Town.

CAPE PROVINCE :—CAPE : Oranjezicht, *Adamson* 1! Rhodes Memorial, *Adamson* 194! Newlands, *Adamson* 195! 255! Rondebosch, *Adamson* 322!

JUNCI GENUINI Buchen. p. 406 (1875), p. 169 (1890), p. 100 (1906); Baker, Flora Cap. vii, p. 17 (1895). *Juncotypus* Dumort. (1827), *vide* T. v. Post & O. Kuntze, Lex. Gen. Phan. p. 303 (1904).

Caespitose perennials. Flowers with prophylls. Leaves basal, all reduced to sheaths. Inflorescence pseudolateral with subtending leaf like continuation of stem.

4. *JUNCUS EFFUSUS* Linn. Sp. Pl. i, p. 326 (1753); Leers, Fl. Herborn. p. 88, t. xiii, 2 (1789); Buchen. p. 228 (1890), p. 135 (1906); Baker, in Fl. Cap. vii, p. 18 (1895); in Flora Trop. Afr. viii, p. 92 (1901).

Perennial, densely tufted with horizontal rhizome. Stems up to 1 m. high. Basal sheaths dull brown. Stem shining, green, smooth, finely striate when dry, pith continuous. Inflorescence much shorter than subtending leaf, effuse or compact, usually without elongated branches. Flowers green or brown, small, c. 2 mm. Perianth equal, acute, external almost subulate, internal lanceolate. Stamens 3,  $\frac{3}{4}$  length of perianth, anthers broad, equalling filament. Capsule obovate, trigonous, retuse, minutely mucronate, shorter than perianth. Seeds yellow, shortly apiculate.

The South African representatives of this species are characterised by very small flowers. They may represent an endemic variety.

Swamps or marshes mostly in the coastal belt, but extending to the interior. Absent from the west coast and the arid regions.

*J. effusus* occurs in Kenya (*vide* Engler, Pflanzenw. Afrik. ii, p. 280 (1908), in Engler & Drude, Veget. d. Erde, ix).

CAPE PROVINCE :—CAPE : Table Mt., *Ecklon* 901! *Moss* 7929! *Adamson* 7! 277! Rondebosch, *Pillans* 3311! Kirstenbosch, *Compton*! *Adamson* 254! Wynberg, *Adamson*! Tokai, *W. Dod* 2191! Hout Bay, *Adamson* 6! Cape Flats, *Adamson* 233! PAARL : Franschhoek, *Moss* 7928! SOMERSET : Boschberg,

*MacOwan* 1964! STOCKENSTROM: Katberg, *Schonland* 4315! E. PONDOLAND : Umzinhlava Riv., *Schlechter* 6553!

NATAL :—DURBAN, *Wood* 13! *Moss* 7044! LION'S RIVER : Howick, *Hutton* 143! Rosetta, *Mogg* 17709! Lidgetton, *Mogg* 877! 3598! 5715! 6822! ESTCOURT : Mooi River, *Wood* 4062! *Mogg* 3227! Balgowan, *Mogg* 5555! 6516! KLIP RIVER : van Reenen, *Bews* 24!

TRANSVAAL :—KRUGERSDORP : Roodepoort, *Moss* 8068! HEIDELBURG : Witpoortje, *Moss* 8355!

5. *JUNCUS ACUTISSIMUS*, sp. n. *J. glaucus* var. *acutissimus* Buchen. p. 417, t. v (1875), p. 244 (1890), p. 133 (1906); Baker, in *Flora Cap.* vii, p. 18 (1895).

Perennis, caespitosa. *Folia* cataphyllina basilaria, basi castanea, superne pallida, nec non nitida. *Caules* obscuri virides vel subglaucescentes, tenuiter striata, medulla interrupta. *Inflorescentia* pseudolateralis folio multo brevior, effusa, ramis subaequalibus vel duplis longioribus. *Flores* ferrugineae, tepalis aequalibus acutissimis subulatis. *Stamina* 6 perianthio duplo breviora, antheris filamenta aequantibus. *Capsula* ovata, trigona, castanea, nitida, perianthio brevior.

This species differs from *J. glaucus* (*J. inflexus*) in so many features—the sheaths, colour, and striation of stem, narrow acute perianth, and length of capsule—that it seems quite worthy of specific rank. Further, it is endemic in South Africa and geographically quite separate from *J. glaucus*, which is not found in the Southern Hemisphere except for records from New Zealand, where it is probably an introduction (cf. G. M. Thomson, 'The Naturalization of Animals and Plants in New Zealand', p. 484 (1922)).

*J. acutissimus* is a smaller plant than *J. glaucus* and forms less dense tufts. The inflorescence is smaller and the flowers smaller and redder.

The type is Drège 8796 c!

Damp places, river-banks, and swamps in the grassland regions at altitudes of 2000 feet and over. Absent from the coast belt, also from the tropical regions and the more arid parts.

CAPE PROVINCE :—KOMGHA, *Flanagan* 1367! QUEENSTOWN : Shiloh, *Baur* 891! 1187! ALBERT : Molteno, *Mogg* 2717! 17462! 17473! WODEHOUSE : Stormberg, *Drège* 8796 b! 'Klein Buffels R., Gaatje', *Drège* 8796 c! ALIWAL NORTH, *Bolus* 58! HERSCHEL : Sterkspruit, *Hepburn* 210! 411!

ORANGE FREE STATE :—WINBURG, *MacOwan* 254! BETHLEHEM, *Flanagan* 2063! *Bolus* 8272!

BASUTOLAND, *Page* 16826!

TRANSVAAL :—Johannesburg, *Moss* 9761! 15838! Burgersdorp, *Flanagan* 1666! 1367!

*JUNCI THALASSICI* Buchen. p. 406 (1875), p. 169 (1890). *Junci thalassii*, p. 100 (1906). *Maritimi*, Baker, in *Flora Cap.* vii, p. 17 (1895). *Acuti*, Fries

Summa. Veg. Scand. i, p. 65 (1846). *Juncastrum* Fourr. in Ann. Soc. Linn. Lyon. xvii, p. 172 (1869). *Juncastrum* O. Kuntze, in T. v. Post & O. Kuntze, Lex. Gen. Phan. p. 303 (1904).

Perennial, caespitose; stems and leaves stiff, pungent. *Leaves* basal, uppermost with cylindrical, stem-like blade. *Inflorescence* terminal or pseudo-lateral, effuse. *Flowers* without prophylls. *Perianth* firm, hard. *Seeds* tailed or appendiculate.

*Key to South African Species.*

- |   |                                 |
|---|---------------------------------|
| 1. Inner perianth retuse. Seeds with large appendages .....                                       | 2.                              |
| Inner perianth obtuse. Seeds tailed .....   | 3.                              |
| 2. Anthers red. Capsule rounded, subspherical, much exceeding perianth .....                      | (6) <i>J. acutus</i> .          |
| Anthers yellow. Capsule ovate, prismatic, just exceeding perianth. Flowers small, clustered ..... | (6a) <i>J. fasciculiflora</i> . |
| 3. Flowers in groups, usually dark. Capsule almost equalling perianth, shortly mucronate .....    | (7) <i>J. Kraussii</i> .        |
| Flowers separate, large, pale. Capsule distinctly exceeding perianth, pointed .....               | (8) <i>J. arabicus</i> .        |

6. *JUNCUS ACUTUS* Linn. Sp. Pl. i, p. 325 (1753). *J. acutus* var. *Leopoldii* Buchen. p. 421, t. v (1875), p. 251 (1890), p. 150 (1906); Baker, in Flora Cap. vii, p. 19 (1895). *J. Leopoldii* Parl. in Giorn. Bot. Ital. ii, p. 324 (1846) (*fide* Buchen.). *J. macrocarpus* Nees, in Linnaea, xx, p. 243 (1847) (nomen).

Densely tufted. *Stems* up to 1 m. *Sheaths* loose, brown, 1 or 2 upper with cylindrical pungent blades as long as stem. *Inflorescence* terminal, effuse, often with one or more elongated branches, subtending leaf pungent, variable in length. *Flowers* solitary or in groups of 2-3. *Perianth* hard, external acute, internal retuse with broad membranous margins. *Stamens* 6, about equal to perianth, anthers red, longer than filament. *Capsule* hard, brown, round-ovate or subglobose, apiculate, about twice length of perianth. *Seeds* with long white appendage.

Buchenau's var. *Leopoldii* was described as having a rounded or spherical capsule not narrowed above. The South African plants have either fruits round or distinctly ovate and pointed above. The two shapes not only grade into one another, but can be found in plants growing adjacent to one another, so that the variety cannot be upheld.

Damp places, especially on salt or alkaline soils. More frequent in the interior and rather dry parts than close to the sea. Confined to the Cape Province.

CAPE PROVINCE :—NAMAQUALAND : Mouth of Orange River, *Ecklon & Zeyher* 73! Henkries, *Schlechter* 20! Pearson 3091! Atties River, *Pearson* 5388! Brak River, *Pearson* 4880! Hondeklip Bay, *Pillans* 18197! 18198! *Bolus* 9475! *Zeyher*! CERES : Verkeerde Vlei, *Rehmann* 2840! WORCESTER : Worcester, *Bolus* 5271! *Adamson* 125! STELLENBOSCH : Somerset West, *Zeyher* 4308! Helderberg, *MacOwan* 1665! SWELLENBOSCH : *Zeyher*! RIVERSDALE : Riversdale, *Muir* 2924! 3381! Kaffir Kuils River, *Muir* 3402! MONTAGU :



Montagu, *Moss* 5381! Kogmans Kloof, *Kunze*! *Michell* 11! LADISMITH: Ladismith, *Adamson* 124! van Wycks Dorp, *Muir* 3361! MURRAYSBURG, *Tyson* 582! RICHMOND: Stylkloof, *Drège, J. acutus*, a, p.pt! GRAAF REINET: Sneuwberg, *Burchell* 2860! HUMANSDORP, *Fourcade* 1747! *E. P. Phillips*! UITENHAGE, *Ecklon*! *Ecklon & Zeyher*! Zwartkops River, *Zeyher* 4311! PT. ELIZABETH: Redhouse, *Rogers* 3606! ALBANY: Grahamstown, *Rogers* 426! BATHURST: Kowie, *Britten* 2125! SOMERSET: Somerset East, *MacOwan*! PEDDIE: Keiskama Mth, *Galpin* 7715! KING WILLIAMS TOWN, *Sim* 162!

UNLOCALISED :—*Thom* 109! *Drège, J. acutus*, g, c. p.pt., d. p.pt.!

6a. *JUNCUS FASCICULIFLORA*, sp. n. Perennis usque ad 40 cm. alta. *Folia* basilaria cataphyllina, straminea, subnitida, summa tria laminifera, laminis cylindricis pungentibus, caule brevioribus. *Inflorescentia* terminalis, effusa, bractea multo longiore. *Flores* parvae, c. 3 mm., in fasciculis terminalibus, 5–6 flor. aggregatae. *Tepala* externa distincte longiora, acuta, interna obtusissima vel retusa marginibus latissimis. *Stamina* sex perianthio duplo breviora, antheris luteis. *Capsula* perianthio paullo longior, straminea, trigona, ovato-prismatica, breviter mucronata. *Semina* longe albo-appendiculata.

Allied to *J. acutus*, but differing in the small flowers aggregated in terminal clusters, the yellow anthers, and the small scarcely exerted capsule.

CAPE PROVINCE :—*CERES*: Zwartruggens, on rocks by waterfall, *Adamson* 123!

7. *JUNCUS KRAUSSII* Hochst. in *Flora N. R.* iii, xxviii, p. 342 (1845) (emend.) ; *Buchen.* p. 418, t. v (1875), p. 255 (1890), p. 153 (1906). *J. maritimus* Baker, *Flora Cap.* vii, p. 19 (1895), p.pt. *J. spretus* Rom. & Schultes, *Syst. Veg.* vii, ii, p. 1656 (1830) (*vide* *Buchenau*).

Perennial, scarcely tufted. *Rhizome* horizontal with close shoots. *Stems* to 40–50 cm., dark green, smooth. *Sheaths* pale brown, upper 1 or 2 with cylindrical, stem-like blades. *Inflorescence* terminal, with subtending leaf longer or shorter, compact or effuse or with long branches. *Flowers* 3–4 mm., pale to dark brown, aggregated in terminal clusters, distinctly but bluntly 3-angled. *Perianth* equal; external concave, acute with broad hard midrib, internal obtuse with membranous margins. *Stamens* 6, shorter than perianth, anthers yellow, much longer than filaments, sometimes abortive. *Ovary* and style red, stigmas long, paler. *Capsule* equalling perianth, trigonous, ovate, dark brown, rounded at top or very shortly mucronate, triseptate. *Seeds* with very short tails.

Var. *EFFUSUS*, nov.

Differt a typo inflorescentia maxima, effusa, floribus majoribus discretis non aggregatis sæpius pallidis.

Var. *PARVIFLORUS*, nov.

Differt a *J. Kraussii* typico, tota planta humiliore, tenuiore, rhizoma elongata, inflorescentia minore effusa, floribus parvis discretis, capsula perianthio brevior

This plant has been much confused with *J. maritimus* Lam., but is readily distinguished by the aggregated, usually dark flowers, which are distinctly but bluntly three-angled owing to the broad blunt keel on the outer perianth. The species is further recognised by the short dark capsule and the seeds with short tails. The variety *parviflorus* is a very distinct-looking plant, more slender in all parts than the type and with much smaller separate flowers.

The type is Krauss's gathered from Zitzikama!

Damp places near the sea, but extending inland to some distance. Commonest in the south and south-west, but extending as far as Lourenço Marques. Not recorded from the west coast north of Table Bay. Var. *parviflorus* occurs on river-banks in the south and south-east coast belts.

CAPE PROVINCE :—PAARL : Klapmuts, *Rehmann* 2266! STELLENBOSCH : Stellenbosch, *Adamson* 166! Hottentots Holland, *Gueinzus*! *Zeyher* 73! CAPE : Cape Town, *Burchell* 252! *Bolus* 484! 4811! *Juncus* 3, *E. M.*! Devils Peak, *Ecklon* 903! Camps Bay, *Burchell* 336! *Adamson* 121! 122! *Moss* 2845! Muizenberg, *Adamson* 174! 175! S. Peninsula, *W. Dod* 2085! *Adamson* 115! 117! 120! 282! 307! Cape Flats, *Moss* 5614! *Rehmann* 1818! Salt River, *Burchell* 677! Koeberg Rd., *Moss* 9154! RIVERSDALE, *Schlechter* 1931! 1969! MOSSEL Bay, *Burchell* 6286! KNYSNA, *Duthie* 903! *Schonland* 3435! 3437! HUMANSDORP : Zitzikama, *Krauss*! UITENHAGE : Zwartkops River, *Ecklon & Zeyher* 647! *Zeyher* 4309! 4310! van Stadensberg, *MacOwan* 2085! PT. ELIZABETH : Redhouse, *Paterson* 1069! 2363! BATHURST : Port Alfred, *Tyson* 160! 13359! *Galpin* 2946! E. LONDON : Kidd's Beach, *Adamson* 299! ALBERT : Molteno, *Mogg* 2718!

NATAL :—Durban, *Rehmann* 8589! Unlocalised, *Buchanan* 126! 364!

PORTUGUESE E. AFRICA :—Lourenço Marques, *Moss* 11772!

UNLOCALISED :—*Harvey* 366! *Drège*, *J. acutus*, f.

Var. EFFUSUS.

CAPE PROVINCE :—HUMANSDORP, *E. P. Phillips*! BATHURST : Port Alfred, *Galpin* 2946! E. LONDON : *Galpin* 7354! KENTANI : Mazeppa Bay, *Hilner* 513! PONDOLAND : Pt. St. Johns, *Schonland* 4307, p.pt.!

NATAL :—Park Rhynie, *Moss* 17088!

Var. PARVIFLORUS.

CAPE PROVINCE :—KNYSNA, *Schonland* 3437! UITENHAGE : Zwartkops River, *Ecklon*! *Meyer* 3! *Ecklon & Zeyher* 90! 903! SOMERSET : Bruin-jeshoogte, *Drège*, *J. acutus*, d, p.pt.! E. LONDON : Buffalo River, *Adamson* 178! 179! 284! KOMGHA : Kei Mouth, *Flanagan* 1778! PONDOLAND : Pt. St. Johns, *Schonland*, 4307, p.pt.! QUEENSTOWN, *Baur* 885! Aliwal North, *Cooper* 1372!

NATAL :—ZULULAND, *Gerrard* 661! *Mogg* 5805! 5809! 5969!

## PORTUGUESE EAST AFRICA :—Matola, Moss 6936!

The type of var. *parviflorus* is Adamson 179!

8. *JUNCUS ARABICUS*, sp. n.

*Juncus maritimus* var. *arabicus* Asch. & Buchen. in Boiss. Fl. Orient v, p. 354 (1882); Buchen. p. 257 (1890), p. 155, fig. 79 (1906). *J. maritimus* Baker, in Flor. Cap. vii, p. 19, p.pt. (1895); in Flor. Trop. Afr. viii, p. 93 (1901).

Perennis usque ad 60 cm. alta, caespitosa. *Folia* cataphyllina straminea, suprema dua vel raro unica laminifera, laminis cylindricis gracilibus caule brevioribus. *Inflorescentia* terminalis vel pseudo-lateralis contracta ramis primariis erectis elongatis, floribus segregatis. *Flores* 4–5 mm. longae. *Tepala* externa distincte longiora acuminata, interna obtusa involuta. *Stamina* 6 perianthio duplo breviora, antheris filamentis triplo longioribus. *Stylus* longus, stigmata rubra exserta. *Capsula* perianthio longe superans trigono-prismatica, apice attenuata, mucronata. *Semina* brevissime appendiculata.

This plant differs from the allied species in the slender stems, generally contracted inflorescence with large, separate, pale flowers, the long style, and distinctly exserted mucronate capsule. It is so distinct in its characters and distribution from *J. maritimus* that it fully deserves specific rank. The original describers of the plant as a variety seemed inclined to this view.

The type is Haussknecht from Egypt.

The plants of this species from southern and tropical Africa are smaller and more slender than many from Egypt, but are otherwise identical.

Damp places on salt or alkaline soils in the interior. Extends through the arid regions and tropics.

CAPE PROVINCE :—NAMAQUALAND, Pearson 5006! 6109! 6079! Pillan's 5523! KURUMAN, Silk 99! 188! GRIQUALAND, W.: Kimberley, Burt Davy 9566! Wilman! Hay, Wilman! Lower Campbell, Burchell 1812! VRYBURG : Vryburg, Burt Davy 11103! RICHMOND : Stylkloof, Drège, *J. acutus*, a, p.pt.! Richmond, Potts 1078! BRITSTIWN : de Aar, Moss & Otley 11580! COLESBURG : Naauwpoort, Rogers 17314! SOMERSET : Witberg, Drège, *J. acutus*, b! ALIWAAL NORTH, Flanagan 1662! ALBERT, Cooper 1372!

TRANSVAAL :—WALMARAANSTAD, Sutton 48!

SW. AFRICA :—Swakop, Galpin & Pearson 7389! 1604! Omaruru, Een!

ANGOLA :—Welwitsch 3007!

N. RHODESIA :—Kafue Flats, Adamson 310! Mumbwa, Adamson 311!

EGYPT, Nolte! Meintzenhagen! Akaba, Hart!

The species in this section have been much confused. Buchenau, in his 1875 monograph, recorded *J. Kraussii* as a S. African plant and also *J. maritimus*. He emended the not wholly satisfactory description of Hochstetter of the former, but included under *J. maritimus* plants referable to

*J. Kraussii* and to *J. arabicus*. Baker in 'Flora Capensis' did not recognise *J. Kraussii* as a species and his arrangement has been followed in herbaria. The real *J. maritimus* Lam. has not been seen in S. Africa, nor have I seen it in any of the herbaria examined. The S. African plants fall into the two distinct species: *J. Kraussii* common in the coastal regions and *J. arabicus* in the interior. Neither is identical with the common seaside plant of Europe.

JUNCI SEPTATI Buchen. p. 406 (1875), p. 169 (1890), p. 101 (1906). *Articulati*, Fries, Summa Veg. Scand. p. 65 (1846); Baker, in Flora Cap. vii, p. 17 (1895); in Flora Trop. Afr. viii, p. 92 (1901). *Ozophyllum* Dumort. (1827), *vide* T. v. Post & O. Kuntze, Lex. Gen. Phan. p. 303 (1904). *Arthrophyllum* Koch, in Linnaea, xxi, p. 628 (1848).

Leaves basal and cauline, unifacial, terete or compressed, septate. Inflorescence terminal with flowers in capitula. Perennial.

*Key to South African Species.*

1. Flowering stem with one leaf. Leaf with central and peripheral air spaces ..... (9) *J. punctorius*.  
    Flowering stems with several leaves, each with central cavity only ..... 2.
2. Capsule distinctly exceeding perianth. Anthers exceeding filaments ..... 3.  
    Capsule less than or just exceeding perianth. Anthers less than filaments ..... 4.
3. Capsule firm, abruptly narrowed to beak. Inflorescence ascending ..... (13) *J. exsertus*.  
    Capsule thin, gradually narrowed to tip. Inflorescence divaricate ..... (14) *J. rostratus*.
4. Style very short or none. Capsule rounded, blunt, or apiculate. (12) *J. brevistylus*.  
    Style as long as ovary. Capsule mucronate ..... 5.
5. Heads dense, spherical. Capsule slightly exceeding perianth, triangular at top, mucronate ..... (10) *J. oxycarpus*.  
    Heads hemispherical. Capsule blunt, sharply mucronate .... (11) *J. suboxycarpus*.

9. JUNCUS PUNCTORIUS Linn. f. Suppl. Pl. p. 208 (1781); Thunb. Prod. Pl. Cap. p. 66 (1794); Buchen. p. 424, t. viii (1875), p. 276 (1890), p. 163 (1906); Baker, in Flor. Cap. vii, p. 20 (1895); in Fl. Trop. Afr. viii, p. 93 (1901). *J. acutiflorus* var. *capensis* Spreng. Neu. Entdeck. ii, p. 107 (1821) (*vide* Buchen.). *J. exaltatus* Decaisne in Ann. Sci. Nat. Bot. 2, ii, p. 16 (1834). *J. Schimperii* Hochst. in Rich. Tent. Fl. Abyss. ii, p. 338 (1847-51) (*vide* Buchen.).

*Rhizome* horizontal. *Stems* up to 1 m., terete, stem and leaves pale green. *Basal leaves* as sheaths, stem leaf one, usually above middle, cylindrical, with lateral and central lacunae. 'Sterile stems' often produced. *Inflorescence* compound, many-headed, primary branches erect, ultimate, divaricate. *Heads* many-flowered, spherical or hemispherical. *Flowers* brown, small, 2-3 mm. *Perianth* equal; external acute; internal obtuse or subacute. *Stamens* 6,

about  $\frac{1}{2}$  perianth. *Anthers* short, oval,  $\frac{1}{2}$  filament. *Capsule* shorter than perianth, ovate, retuse, mucronate, brown.

The 'sterile stem', in which the leaf is very long, may develop the following year, giving the appearance of more than one leaf on the flowering stem. The form of inflorescence varies, being an effuse panicle or compacted, but the species is very distinct and easily recognisable.

Swamps and river-banks, where moisture is permanent. Generally distributed, but often local. Extends to N. Africa and Arabia.

CAPE PROVINCE :—NAMAQUALAND : Henkries, *Schlechter*! Atties River, *Pillans* 5389! Eselsbank, *Drège*, *J. oxyc.*, g! CLANWILLIAM : Wupperthal, *Drège*, *J. oxyc.*, f! Oliphants River, *Drège*, *J. oxyc.*, e! CERES : Ceres, *Pearson* 3558! TULBAGH : Waterfall, *Ecklon* 46! WORCESTER, *Rehmann* 2549! Hex River, *Tyson* 823! PAARL : Klapmuts, *Rehmann* 2265! Paarl, *Drège* aa! STELLENBOSCH : Stellenbosch, *Ecklon* 83! *Adamson* 154! 155! Jonker's Hoek, *Adamson* 14! 15! 16! Hottentots Holland, *Gueinzinus*! *Zeyher* 140! Firgrove, *Adamson* 140! Stickland, *Adamson* 165! CAPE : Cape Town, *Burchell* 253! 674! Table Mt., *Ecklon* 47! 902! S. Peninsula, *W. Dod* 3446! *Michell*! Cape Flats, *Adamson* 261! SWELLENDAAM : Swellendam, *Mundt* 91! Barrydale, *Barnard*! KNYSNA : Knysna, *Fourcade*! UNIONDALE, *Fourcade* 1724! HUMANSDORP : Karriedouw, *Britten* 1259! Uitenhage : Zwartkops River, *Zeyher* 648! Bethelsdorp, *Drège*, *J. oxyc.*, h! KING WILLIAMS TOWN, *Hilner* 124! E. LONDON : Fort Grey, *Adamson* 293! KOMGHA, *Flanagan* 978! Umtata, *Drège*, *J. oxyc.*, i! ABERDEEN : Camdeboosberg, *Drège*, *J. oxyc.*, c! SOMERSET : Fish River, *MacOwan*, 1715! MIDDELBURG, *Gill* 19! ALIWAL NORTH, *Bolus* 217! GRIQUALAND, W. : Griquatown, *Burchell* 1871!

ORANGE FREE STATE :—VREDEORT : *Parys*, *Rogers* 209!

BASUTOLAND :—Leribe, *Dieterlen* 767 a! 685 b! Mafeteng, *Dieterlen* 1314!

TRANSVAAL :—WALMARAANSTAD, *Sutton* 104! BURGHERSDORP, *Flanagan* 1665! JOHANNESBURG, *Rand* 1031! HEIDELBERG : Henly on Klip, *Moss* 17332! PRETORIA, *Rehmann* 4472! 4473! Aapias River, *Schlechter* 3615!

NATAL :—NEWCASTLE : Mt. aux Sources, *Bayer & McClean* 121! DUNDEE, *Truscott* 149! BERGVILLE, *Galpin* 9502!

UNLOCALISED :—*Zeyher* 4976!

N. AFRICA :—SOMALILAND, *Godman* 124! ABYSSINIA, *Schimper* 56!

ASIA :—ARABIA, *Schimper* 279!

10. *JUNCUS OXYCARPUS* E. Mey. in Kunth, Enum. Pl. iii, p. 336 (1841); Buchen. p. 431, t. viii (1875), p. 336 (1890), p. 196 (1906); Baker, in Flor. Cap. vii, p. 20 (1895); in Fl. Trop. Afr. viii, p. 93 (1901). *J. acutiflorus* Spreng. Neu. Entdeck. ii, p. 107 (1821) (non Ehrh., fide Buchen.).

*Rhizomes* short, *stems* usually isolated, to 50 cm., terete or subcompressed. *Leaves* cauline, 3-4, shorter than stem. *Inflorescence* few-headed, umbellate-paniculate. *Heads* many-flowered, 15-25, spherical. *Flowers* 3-4 mm. *Perianth* subequal; external acute or acuminate; internal subacute. *Stamens* 3 opposite outer perianth. *Anthers* ovate,  $\frac{1}{2}$  length of filaments. *Style* equalling ovary, stigmas long. *Capsule* equalling or slightly exceeding perianth, dark brown, trigonous, acute, mucronate. *Seeds* shortly apiculate.

Var. MICROCEPHALUS, nov.

Differt *J. oxycarpo* typico, inflorescentia umbellata; capitulis numerosis, minoribus, paucifloris (3-7); capsula perianthium aequante, longe mucronata.

Damp places, river-banks, and swamps. Generally distributed, absent in arid regions. Recorded from Central Africa. The commonest of the *J. septati*.

CAPE PROVINCE:—WORCESTER: Worcester, *Rehmann* 2551! Bains Kloof, *Schlechter* 10259! TULBAGH: Tulbagh Kloof, *Adamson* 23! PAARL: Paarl, *Drège*, a! *Rehmann* 2256! Franshhoek, *Moss* 7926! STELLENBOSCH: Elsenburg, *Marloth*! Stellenbosch, *Adamson* 153! Jonker's Hoek, *Adamson* 17! 19! 22! Hottentots Holland, *Zeyher*! Sir Lowry Pass, *Adamson* 128! CAPE: Table Mt., *Adamson* 18! 270! 272! 278! Salt River, *Burchell* 672! Wynberg, *Drège*, *J. oxyc.*, d! Kirstenbosch, *Adamson* 252! 253! Constantia, *W. Dod* 2051! S. Peninsula, *W. Dod* 3248! 3267! *Levy*ns! CALEDON: Grabouw, *Bolus* 4217! Onrust, *Adamson* 24! SWELLENDAM: Tradouw Pass, *Schlechter* 2084! RIVERSDALE, *Schlechter* 1938! *Burchell* 6551! KNYSNA: Deepwalls, *J. Phillips* 28! OUDTSHOORN: Swartberg Pass, *Adamson* 300! 302! UITENHAGE: Zwartkops River, *Zeyher* 5! Uitenhage, *Paterson* 2159! ALBANY: Grahamstown, *Daly & Cherry* 973! *Daly & Sole* 134! STOCKENSTROM: Hogsback, *Ratray* 393! E. LONDON: Fort Grey, *Adamson* 295! KENTANI: Kentani, *Pegler* 1000! 202! PONDOLAND: Pt. St. Johns, *Moss* 2843! MACLEAR, *Britten* 4590! MT. CURRIE: Kokstad, *Mogg* 5134! 18701!

BASUTOLAND:—Leribe, *Dieterlen* 767! 4735!

SWASILAND:—Mbabane, *Rogers* 11624!

ORANGE FREE STATE:—HEILBRON: Vaal River, *Brandmuller* 9! HARRISMITH: Witzieshoek, *Bolus* 8273!

TRANSVAAL:—JOHANNESBURG, *Rand* 914! Alberton, *Moss* 12053! Birchleigh, *Moss* 14410! Florida, *Moss* 9810! *Hutton* 822! Rietfontein, *Moss* 16562! HEIDELBERG: Witpoortje, *Moss* 8330! PRETORIA: *Verdoorn* 5! *Moss* 10529! Waterkloof, *Mogg* 15603! ERMELO, *Potter* 1780! *Henrici* 1444! WAKKERSTROM: Volksrust, *Mogg* 7454! UNLOCALISED, *Burt* *Davy* 17358! 17694!

NATAL:—LION'S River: Lidgetton, *Mogg* 878! ESTCOURT: Mooi River, *Mason* 7946! *Mogg* 3367! 7018! Tweedie, *Mogg* 6778! BERGVILLE: Tugela

River, *Galpin* 11436! Mt. aux Sources, *Bayer & McClean* 93! Clairmont, *Wood* 9614! Umzinyati River, *Wood* 1053!

CENTRAL AFRICA :—S. RHODESIA : Salisbury, *Eyles* 1891! RUENZORI, *Scott Elliott* 6623!

Var. MICROCEPHALUS.

CAPE PROVINCE :—RIVERSDALE : Oakdale, *Muir* 3385! HUMANSDORP : Louwbosch River, *Fourcade* 1091! ALBANY : Grahamstown, *Dyer* 173! SOMERSET : Somerset East, *Rennie*! STUTTERHEIM : Dohne Hill, *Sim* 2847!

ORANGE FREE STATE :—BETHLEHEM, *E. P. Phillips*!

NATAL :—Caversham, *Webb* 8925! Clairmont, *Wood* 9614! Mooi River, *Mogg* 3214! Dargle Road, *Mogg* 5738! Lidgetton, *Mogg* 878!

# 11. JUNCUS SUBOXYCARPUS, sp. n.

*Caules* teretes, 10–30 cm. alti. *Folia* caulina 3–4 subcompressa, septata, laevia, caulibus breviora. *Inflorescentia* composita, capitula numerosa, in summis ramis congesta vel conglobata, multiflora aut rarissime hemisphaerica. *Flores* c. 3 mm. longae, castaneae vel ferrugineae. *Tepala* aequilonga, acuta; interna marginibus albomembranaceis involutis. *Stamina* 3, perianthio duplo breviora, antheris parvis, filamentis duplo brevioribus. *Stylus* brevis. *Capsula* perianthio paullo brevior vel aequans, trigona, obtusa, abrupte mucronata. *Semina* parva ovata brevissime apiculata, reticulata.

Allied to *J. oxycarpus*, but distinguished by the smaller, more numerous heads, which are not spherical and are often crowded at the tops of the inflorescence branches, by the obtuse, abruptly mucronate capsule, and the smaller seeds. The whole plant is smaller and more slender than *J. oxycarpus*. The name was applied by the late Professor C. E. Moss in manuscript notes. The type is Schlechter 3043.

Damp places, marshes, and river-sides. More common in the eastern parts.

CAPE PROVINCE :—Hottentots Holland, *Gueinzins*! Botha Valley, *Schonland* 4423! Cathcart, *Cotterell* 60! Queenstown, *Moss* 19995!

NATAL :—Clairmont, *Schlechter* 3043! Pietermaritzburg, *J. Wahlberg*! Unlocalised, *Wilms* 2326!

TRANSVAAL :—Houghton, Johannesburg, *Moss* 6723!

UNLOCALISED :—Good Hope, *Wahlberg*!

ANGOLA :—Huilla, *Wehwitsch* 3008!

12. JUNCUS BREVISTYLUS Buchen. p. 433, t. viii (1875), p. 346 (1890), p. 209 (1906); Baker, in *Flora Cap.* vii, p. 20 (1895). *J. gentilis* N. E. Br. in *Kew Bull.* 2, p. 83 (1914).

Tufted, generally small, 10–20 cm., occasionally 40 cm. *Leaves* slender with distinct auricles, 2–3 on flowering stem. *Inflorescence* few heads, 4–7. *Heads* many-flowered, hemispherical. *Flowers* 3 mm., brown. *External perianth* acute or mucronate, slightly longer than obtuse, involute internal, both with broad membranous margins. *Stamens* 3,  $\frac{1}{2}$  perianth. *Anthers*  $\frac{1}{2}$  length of filaments. *Style* very short. *Capsule* slightly less than perianth, ovate, rounded, very shortly apiculate.

Damp places, marshes, or stream-sides in the High Veld grassland region. Absent from the coastal belt and the western regions. Endemic to S. Africa.

ORANGE FREE STATE :—HARRISMITH : Witzies Hoek, *Flanagan* 2052!

TRANSVAAL :—KRUGERSDORP, *Moss* 11359! JOHANNESBURG, *Moss* 12053! HEIDELBERG, *Schlechter* 3529! Witpoortje, *Moss* 2255! 7986! PRETORIA, *Rogers* 18974! Wonderboom, *C. A. Smith* 2267! Silverton, *Moss* 8499! Modderfontein, *Conrath* 1173! ERMELO : Lake Chrissie, *Moss* 16894!

NATAL :—NEWCASTLE, *Schlechter* 3427! KLIPS RIVER : van Reenen, *Bews* 25! UMGENI : Pietermaritzburg, *J. Wahlberg*!

BASUTOLAND :—Leribe, *Dieterlen* 921!

13. *JUNCUS EXSERTUS* Buchen. p. 435 (1875), p. 337 (1890), p. 196 (1906); Baker, in *Flora Cap.* vii, p. 21 (1895).

Caespitose, generally smaller than *J. oxycarpus*. *Leaves* slender, short. *Inflorescence* spreading and ascending, many-headed. *Heads* few-flowered (3–8–12). *Flowers* c. 3 mm. *Perianth* about equal; external mucronate; internal involute, pseudoacute. *Stamens* 3 or 6,  $\frac{1}{2}$ – $\frac{3}{4}$  perianth. *Anthers* elongate, equalling or exceeding filaments. *Capsule* elongate,  $1\frac{1}{2}$ –2 times perianth, 3-angled, with depressed sides, narrowed at top to 3-angled beak about  $\frac{1}{2}$  length of capsule. *Seeds* reticulate, distinctly apiculate.

This species varies in the numbers of flowers in the capitula. The commonest forms have few (three to five). Forms with three and with six stamens occur growing together. No other differences are correlated with the number of stamens.

The type is Zeyher 103!

Swamps and river-banks mostly in the eastern parts. Extends through the interior to S. Rhodesia. Rare in the western parts.

CAPE PROVINCE :—WORCESTER : Worcester, *Zeyher*! OUDTSHOORN : Kamanassie, *Britten* 3083! Meirings Poort, *Adamson* 185! 187! MURRAYSBURG, *Tyson* 583! GRAAF REINET : Sundays River, *Bolus* 188! SOMERSET : Somerset East, *MacOwan* 1779! *Bowker*! STOCKENSTROM : Katberg, *Adamson* 305! KING WILLIAMS TOWN, *Leighton* 8! STUTTERHEIM : Dohne Hill, *Sim* 2849! CATHCART : Toise River, *Hilner* 523! 372! p.pt. KOMGHA : Kei Mouth, *Flanagan* 1368! QUEENSTOWN : Queenstown, *Galpin* 2420! *Hilner* 355!



Shiloh, *Baur* 777! 852! Tbeka, *Schlechter* 6254! Mt. CURRIE : Kokstad, *Mogg* 5141! 1636! ALIWAL NORTH, *F. Bolus* 273! GRIQUALAND WEST : Kimberley, *Burt Davy* 9566! Warrenton, *Wilman*! Hay, *Wilman*! Daneelskuil, *Wilman*! Griquatown, *Burchell* 1906! VRYBURG, *Mogg* 8437! KURUMAN, *Silk* 169!

ORANGE FREE STATE :—BLOEMFONTEIN, *Potts* 2871! 2174! KROONSTADT, *Pont* 509! *Moss* 19389! HERBERT : *Anderson* 685! UNLOCALISED, *Rehmann* 3762!

BASUTOLAND :—Leribe, *Dieterlen* 685! 685 a! 6988! *Page*!

NATAL :—LIONS RIVER : Rosetta, *Mogg*! NEWCASTLE : Ingogo, *Mogg* 7582! ZULULAND, *Salisbury & Carson*!

TRANSVAAL :—WALMARAANSTAD, *Sutton* 105! JOHANNESBURG, *Rand* 1032! *Moss* 5953! 6722! van Wycks Rust, *Moss* 19988! HEODELBERG : Witpoortje, *Moss* 8329! 10139! PRETORIA, *Mogg* 11762! 11810! 15602! *Moss* 2844! 15733! *Verdoorn* 2! Wonderboompoort, *Rehmann* 4471! 6698! C. A. *Smith* 1426! Aapies River, *Schlechter* 3640! Onderstepoort, *Theiler* 9690! Witfontein, *Moss* 18405! CAROLINA, *Moss & Rogers* 1106 bis! ERMELO, *Henrici* 1351! *Potts* 1767! E. TRANSVAAL, *Nelson* 320!

UNLOCALISED :—*Burchell* 582! *Drège*, *J. oxycarpus*, d! *Tyson* 1791! *Zeyher* 103! 362! 4313!

SW. AFRICA :—Otavi, *Dinter* 5318!

S. RHODESIA :—Salisbury, *Eyles* 587! 1539!

14. *JUNCUS ROSTRATUS* Buchen. p. 437 (1875), p. 338 (1890), p. 196 (1906); Baker, in *Flora Cap.* vii, p. 21 (1895).

Perennial, tufted. *Flowering stems* inclined or spreading, not erect. *Leaves* slender. *Inflorescence* spreading, branches often recurved, ultimate divaricate. *Heads* few-flowered. *Perianth* equal; external shortly aristate; internal acute. *Stamens* 3,  $\frac{1}{2}$ — $\frac{3}{4}$  perianth, anthers equalling or exceeding filaments. *Capsule* trigonous, slender, gradually narrowed from the base to tip, brown, double length of perianth, thin and translucent at base. *Seeds* apiculate.

This species is very closely allied to *J. exsertus* and especially to the three-stamened forms. It is distinguished most readily by the capsule, which is gradually narrowed to the tip and not beaked. The inflorescence is more divaricate with separate few-flowered heads and the internal perianth is less aristate and more acute. The difficulties of distinguishing the two species have been increased by Buchenau's figures (l.c. (1875), t. v), where the capsule of *J. rostratus* is represented as much more distinctly beaked and shorter than in typical representatives.

Specimens intermediate between the two species may possibly be hybrids, but further study in the field is required before their true position can be determined. Such intermediates are : *Schlechter* 3949, Lydenburg; *Mogg* 1036 and 18703, Kokstad.

The type in Ecklon from Zwartkops River.

Swamps and marshes in the eastern parts. Absent from the western Cape.

CAPE PROVINCE:—UITENHAGE: Zwartkops River, *Ecklon*! EAST LONDON: Fort Grey, *Adamson* 294! 295! KOMGHA: Kei River, *Flanagan* 985! TRANSKEI: Bashee River, *Drège* 4465! Umtata, *Schlechter* 6348! MT. CURRIE: Kokstad, *Mogg* 18703! *Tyson* 923!

NATAL:—ESTCOURT: Mooi River, *Mogg* 219! 7017! 7242! Balgowan, *Mogg* 3862! 3868! Tugela River, *Galpin* 9503! UNLOCALISED, *Buchanan* 67! 358!

BASUTOLAND:—Leribe, *Dieterlen*, 683 p.pt.!

SWAZILAND:—PIETERSBURG: Houtbosch, *Rehmann* 5741! WAKKERSTROM: Volksrust. *Mogg* 7453!

JUNCI GRAMINIFOLII Buchen. p. 441 (1875), p. 170 (1890), p. 101 (1906); Baker, in *Flora Cap.* vii, p. 17 (1895), p.pt. *Junci singulares* Buchen. p. 438 (1875); p. 170 (1890), p. 101 (1906), Vierhapper, in Engler & Prantl, *Die Nat. Pflanzenf.* 15 a, Auf. 2, p. 216 (1930). *Cephaloxys* Desv. in *Journ. de Bot.* i, p. 321 (1808). *Singularia* O. Ktze. in T. v. Post & O. Kuntze, *Lex. Gen. Phan.* p. 303 (1904).

*Flowers* without prophylls. *Inflorescence* terminal, one- or many-headed. *Leaves* all basal, flat or channelled above.

## A. PERENNIAL SPECIES.

### *Key to perennial species.*

- |   |                                |
|---|--------------------------------|
| 1. Sheaths closed. Leaves broad, flat, 5–8 mm. or more .....                                      | 2.                             |
| Sheaths split. Leaves narrow, flat, or channelled .....   | 3.                             |
| 2. Leaves glaucous. Sheaths red. Inflorescence many-headed .                                      | (15) <i>J. lomatophyllus</i> . |
| Leaves green, shining. Sheaths yellow. Inflorescence few-headed .....                             | (16) <i>J. viridifolius</i> .  |
| 3. Style short or none. Anthers shorter than filament .....                                       | 4.                             |
| Style at least as long as ovary. Anthers equal to or longer than filaments .....                  | 6.                             |
| 4. Head many-flowered, spherical or hemispherical .....   | 5.                             |
| Heads fewer-flowered, cuneate below .....   | (18) <i>J. Subcuneatus</i> .   |
| 5. Heads 1–5, separate or crowded. Leaves flat .....  | (17) <i>J. Dregeanus</i> .     |
| Head usually 1, compound, asymmetric. Leaf narrow linear. Flowers dark. Densely tufted .....      | (19) <i>J. subglobosus</i> .   |
| 6. Leaves flat or channelled, 3–5 mm. broad. Loosely tufted .                                     | 7.                             |
| Leaves narrow, inrolled. Densely tufted or caespitose .....                                       | 12.                            |
| 7. Heads small. Flowers small. Capsule broad, rounded, almost equalling perianth .....            | (20) <i>J. indescritus</i>     |
| Heads larger. Flowers larger. Capsule shorter than perianth, oval or prismatic, not rounded ..... | 8.                             |
| 8. Capsule apiculate .....  | 9.                             |
| Capsule distinctly mucronate or rostrate .....  | 10.                            |

9. Heads few. Flowers large. Turf-forming. Leaves short . . . (21) *J. Sonderianus*.  
 Heads many. Inflorescence divaricate. Leaves soft . . . . . (23) *J. apiculatus*.  
 10. Tall, many-headed. Heads hemispherical squarrose in fruit . . . (22) *J. anonymus*.  
 Shorter. Heads few, umbellate, many-flowered, but not  
 squarrose . . . . . 11.  
 11. Leaf flat, channelled, dark green. Flowers pale outside,  
 dark within . . . . . (27) *J. atropurpureus*.  
 Leaf unifacial, minutely channelled above, more or less  
 distichous . . . . . (26) *J. singularis*.  
 12. Caespitose. Leaf narrow, soft. Stems exceeding leaves.  
 Heads many. Capsule narrow, mucronate . . . . . (24) *J. capensis*.  
 Turf-forming. Leaf linear, often equalling stems. Heads  
 few. Flowers pale. Capsule mucronate, broad . . . . . (25) *J. sphagnetorum*.

15. *JUNCUS LOMATOPHYLLUS* Spreng. in Neue Entdeck. . . Pflanzenkunde, ii, p. 108 (1821) ; Kunth, Enum. Pl. ii, p. 343 (1841) ; Steudel, Sym. Pl. Glum. ii, p. 303 (1855) ; Buchen. p. 466 (1875), p. 429 (1890), (1906) p. 247 ; Baker, in Flora Cap. vii, p. 27 (1895). *J. cephalotes* Spreng. in Linn. Syst. Veg. ii, p. 106 (1825). *J. capensis* var. *latifolius* E. Mey. Syn. Junc. p. 48 (1822). *J. cymosus* Lamk. Enc. Meth. Bot. iii, p. 267 (1789) (species mixta et dubia, *fide* Buchen. p. 469 (1875).

Perennial, tufted with leafy offshoots. *Stems* scapose to 80 cm. high. *Leaves* broad, 8–15 mm., flat, with closed sheath, glaucous, sheaths red. *Inflorescence* many-headed, umbellate, paniced. *Heads* 3–12-flowered. *Bracts* aristate. *Flowers* 3–4 mm. ; perianth subequal or external longer ; external acuminate or aristate ; internal obtuse, involute. *Stamens* 6, about  $\frac{3}{4}$  perianth. *Anthers* double length of filaments. *Style* long, stigmas red, exserted. *Capsule*  $\frac{1}{2}$ – $\frac{3}{4}$  perianth, dark brown, narrow above, rostrate.

Var. *TYPICUS* Buchen. p. 430 (1890).

*Inflorescence* umbellate, ascending. *Heads* small. *Flowers* dark. *Perianth* subequal.

Var. *LUTESCENS* Buchen. p. 466 (1875).

Tall, luxuriant. *Leaves* long. *Inflorescence* very many headed, heads larger, many-flowered. *Flowers* pale.

Var. *CONGESTUS*, nov.

*J. lomatophyllus* var. *aristatus* Buchen. p. 466 (1875), p.pt. Differt a var. *typico*, capitulis minus numerosis, multifloris, sphaericis vel hemisphaericis ; floribus majoribus, castaneis, tepalis externis longioribus, aristatis ; capitulis saepe congestis.

*J. lomatophyllus* is one of the commonest and most widespread of the South African species. It is probably the best known, and is certainly the most easily recognised. This being so, it is surprising that none of the older writers distinguished it at all clearly. For the synonymy and the determinations of

Thunberg's two poorly defined species, I have followed Buchenau, who fully discusses the problem (pp. 468-74 (1875)). By doing so, the generally accepted usage is maintained and a clear starting definition is obtained for this very distinct species.

In herbaria small specimens of the plant are sometimes confounded with the annual *J. cephalotes* Thunb.

Stream-sides and by running water, less often in marshes. Generally distributed through the country. Ascends as high as springs occur on mountains. Absent from the drier regions.

*Var. typicus.*

CAPE, SW.:—PIQUETBERG: Pickeneer's Kloof, *Pearson* 5236! CAPE: Table Mt., *Ecklon* 50! *MacGillivray* 420! 421! *Adamson* 33! 126! Kirstenbosch, *Adamson* 240! 241! Wynberg, *Ecklon*! Clifton, *Moss* 7934! PAARL: Paarl, *Drège*! Gr. Drakenstein, *Rogers* 10528! WORCESTER: Du Toits Kloof, *Drège*, *J. cap.*, var. a! STELLENBOSCH: Stellenbosch, *N. J. Andersson*! Sir Lowry Pass, *Andreae* 42! Hottentots Holland, *Gueinzius*! CALEDON: Grabouw, *Bolus* 4219! Houwhoek, *Penther* 354! SWELLENDAM: Swellendam, *Adamson* 325! RIVERSDALE: Riversdale, *Muir* 2815! *Schlechter* 1933! MONTAGU: Montagu, *Adamson* 34! OUDTSHOORN: Swartberg Pass, *Adamson* 182!

CAPE, E.:—HUMANSDORP: Zitzikama, *Fourcade* 108! Humansdorp, *E. P. Phillips*! Uitenhage: Sunday's River, *Gill*, p.pt.! Uitenhage, *Zeyher* 442! *Burchell* 4271! Zwartkops River, *Drège*, *J. cap. latif.*, d! *Drège*, *J. cap. latif.*, e, p.pt.! ALBANY: Howiesons Poort, *Schonland*! Grahamstown, *MacOwan*! *Schonland* 441! Trapp's Valley, *Daly* 689! De Kol, *Grant* 39! STOCKENSTROM: Katberg, *Moss* 15335! K. WILLIAM'S TOWN: Keiskamahoe, *Dyer* 314! E. LONDON: East London, *Thode* 6572! KENTANI: Kentani, *Pegler* 1103! 1305! TEMBULAND: Baziza River, *Baur* 543! KOMGHA: Komgha, *Flanagan* 975! 1006! E. GRIQUALAND: *Tyson* 2866!

NATAL:—ALEXANDRIA: *Rudatis* 766! DURBAN: Durban, *Rehmann* 8590! Umbilo, *Wood* 12001! UMGENI: P. M. Burg, *Mogg* 2252! *J. Wahlberg*! *Wilms* 2324! Howick, *Hutton* 190! 453! LIONS RIVER: Dargle Road, *Mogg* 5711! Tweedie, *Mogg* 6777! ZULULAND: *Mogg* 6080! UNLOCALISED, *Wood* 221! 7657! *Gerrard* 494! *Rehmann* 8591! *Rudatis* 760.

TRANSVAAL:—JOHANNESBURG: Florida, *Moss* 15931! HEIDELBERG: Witpoortje, *Moss* 6445! 9754! LYDENBURG: Graskop, *Pole Evans*! PIETERSBURG: Pietersburg, *McCallum* 137!

*Var. lutescens.*

CAPE, SW.:—CAPE: Table Mt., *Ecklon* 25! *Macowan* 1990! *Marloth* 3275! 3899! WORCESTER: Du Toits Kloof, *Drège*, *J. cap. latif.*, a! Hex River, *Tyson*! CALEDON: Elgin, *C. A. Smith* 2530!

CAPE, EAST :—ALBANY : Grahamstown, *Daly & Cherry* 972! STOCKENSTROM : Katberg, *Sole* 425!

NATAL :—ZULULAND : *Mogg* 5753!

Var. *congestus*.

CAPE, SW. :—CAPE : Cape Town, *Drège, J. cap. latif.*, e, p.pt.! *Guthrie* 1387! *Mogg* 1113737! Table Mt., *Marloth*! *Adamson* 271! Devils Peak, *Kunze*! OUDTSHOORN : Swartberg Pass, *Adamson* 181!

CAPE, E. :—UITENHAGE : Zwartkops River, *Drège, J. cap. latif.*, e, p.pt.! ALBANY : Grahamstown, *MacOwan* 689! PEDDIE : Keiskama Mth., *Galpin* 7682! E. LONDON : East London, *Hilner* 152!

NATAL :—DURBAN : Umbilo, *Wood* 12001! ZULULAND : Homewith, *Mogg* 5898!

TRANSVAAL :—LYDENBURG : Graskop, *Pole Evans*! UNLOCALISED, *Wilms* 1565! 1567!

UNLOCALISED :—*Ecklon* 896! *Pappe* 112!

*J. lomatophyllus* is recorded for tropical Africa (cf. *Baker, Flora Trop. Afr.* viii. p. 14 (1901); *Buchen.* p. 248 (1906)), but the identifications are by no means certain, and may quite possibly refer to one of the allied species, *J. Engleri* *Buchen.* or *J. Bachiti* *Hochst.* (cf. *Engler, Die Pflanzenw. Afrik.* ii, p. 281, in *Engler & Drude, Die Veget. der Erde*, ix, 1908).

This species is also found in St. Helena (cf. *Buchen.* p. 430 (1890), where it is probably originally an introduction from S. Africa.

#### 16. *JUNCUS VIRIDIFOLIUS*, sp. n.

*Juncus lomatophyllus* var. *aristatus* *Buchen.* p. 466 (1875), p. 430 (1890), p. 248 (1906), p.pt.

*Juncus lomatophyllus* auct., p.pt.

*Juncus lomatophyllus* var. *viridifolius* *Andreae* in herb.

Affinis *J. lomatophyllus*. *Caules* breviores, usque ad 40 cm., caespitosa, rami steriles proliferes desunt vel brevissimi. *Folia* viridia, nitida, usque ad 20 cm. longa et 5–10 mm. lata, vaginis stramineis non rubris. *Inflorescentia* terminalis, paucicapitata (1–8), ramis erectis vel erecto-patentibus. *Capitula* hemisphaerica, multiflora (6–15) longe pedunculata. *Bractea* infima frondescens inflorescentia multo brevior, capitulo infimo paullo longior. *Bracteae* florum longe acuminatae floribus breviores. *Flores* 3–4 mm. longae, saepius castaneae. *Tepala* aequalia, externe aristata. *Stamina* 6, tepalis duplo vel triplo breviora. *Capsula* straminea vel brunnea perianthio brevior. Caetera ut in *J. lomato-phylo*.

This species differs from *J. lomatophyllus* in the more closely tufted habit without long offshoots, and the shining green leaves which are not at all glaucous. The leaves are generally rather narrower. The sheaths are yellowish, not red.

The inflorescence is of few, many-flowered heads on stout branches. The stamens are shorter and the capsule paler.

*J. viridifolius* is a smaller plant than *J. lomatophyllus* and seems confined to mountain streams. It flowers two to three weeks earlier than *J. lomatophyllus*.

The type is Adamson 247!

Stream-sides on mountains in the South Western districts. The plant descends to 1,000 feet or less, but does not extend to the plains.

CAPE PROVINCE :—CAPE : Cape Town, *N. J. Andersson!* *Debeaux!* Table Mt., *Drège, J. cap. latif.*, f, g, i! *Compton!* *Andreae!* Adamson 32! 127! 244! 247! 249! 276! 279! 280! 281! Devils Peak, Adamson 196! Simons Bay, *Milne* 225! PAARL : Gt. Drakensteen, *Rogers* 10528! WORCESTER : Bains Kloof, *Bolus* 4080! TULBAGH : Tulbagh, *E. P. Phillips!* OUDTSHOORN : Swartberg Pass, Adamson 301! UNLOCALISED : Afr. Aust. *J. Wahlberg!* Iter Austr. *R. Brown!* *Drège, b!* *Zeyher* 14! *Rehmann* 9644!

17. *JUNCUS DREGEANUS* Kunth, Enum. Pl. iii, p. 344 (1841) (emend.); Buchen. p. 462, t. ix (1875); Buchen. p. 436 (1890), p. 251 (1906); Baker, in *Flora Cap.* vii, p. 25 (1895). *J. cephalotes* Thunb. Prodr. Pl. cap. p. 66 (1794), p.pt.

Perennial, tufted. *Leaves* linear, flat, inrolled when dry. *Sheaths* a quarter or less length of blade, with narrow membranous margins and no auricles. *Stems* 3–4 times length of leaves, 15–40 cm., slender, terete, finely striate. *Inflorescence* of 1–5 heads, crowded and sessile or the lateral stalked. *Heads* hemispherical or nearly spherical, many-flowered. Lowest bract leaf-like, equalling or exceeding the heads. *Flowers* small, 3–5 mm., pale or brown, rarely black. *Perianth* about equal; external mucronate or shortly aristate; internal with broad, membranous, incurved margins. *Stamens* 3–4–6,  $\frac{1}{2}$  length of perianth, anthers equalling or less than filaments. *Style* very short, stigmas red. *Capsule*  $\frac{2}{3}$  perianth, obovate, obtuse, very shortly apiculate. *Seeds* small, round-oval, very shortly apiculate.

Var. *GENUINUS* Buchen. p. 463 (1875) (emend.).

Caespitose. *Leaves* narrow, much shorter than slender stems. *Flowers* small, 3 mm. *Capsule* rather flattened on top, shortly mucronate. *Seeds* round-oval.

Var. *SPHAEROCEPHALUS*, nov.

Differt *J. Dregeano* habitu robustiore, subcaespitoso vel solitario; *foliis* latioribus vaginis amplioribus; *capitulis* densis multifloris, sphaericis vel hemisphaericis, pedunculatis vel congestis; *floribus* majoribus c. 4 mm.; *antheris* brevioribus; *capsula* apice rotundata breviter apiculata et *seminibus* asymmetricis.

Var. *LONGISTYLUS*, nov.

Var. *sphaerocephalo* similis sed differt *floribus* majoribus, pallidis, in capitulis magnis sphaericis, 8–9 mm. diametro, lateralibus pedunculatis, dispositis;

*staminibus* 6, antheris filamentis triplo brevioribus; *stylo* longo, *stigmatibus* rubris exsertis; *capsula* obtusa breviter mucronata.

Known only from collections of E. Kensit from Cape Peninsula.

The type of *J. Dregeanus* is Drège 4387, co-type Drège 1604, i!

Under *J. Dregeanus* Kunth, Buchenau (l.c. 1875) distinguished three varieties. Var. a. *genuinus* and var. b. *conglomeratus* differ only in the presence or absence of peduncles to the lateral heads. Plants that would come under both varieties are found growing together, and every stage of intermediate can be found. There seems no valid reason for separating these two. Specimens quoted by Buchenau show no distinguishing features except the peduncles, e.g. Drège 1604, i, as var. *genuinus*, and Ecklon and Zeyher 'Hassagaibosch', the type of var. *conglomeratus*. Buchenau's third variety, *submonocephalus*, is diagnosed 'planta parva, inflorescentia e capitulis paucis conglobata. *J. submonocephalus* Steud. Syn. Glum. 1855, ii, p. 303? (Drège 1604, f)! '.

The specimen quoted is a small plant with a single compound head. It agrees with var. *genuinus* in leaf and seed characters and in size of flowers, but has capsules more rounded on top. This alone is not sufficient to give the plant varietal rank. *J. submonocephalus* Steud. is an uncertain plant which is incompletely described. From the notes it is evident that Steudel was describing a plant allied to *J. capensis*. He quotes '*J. capensis* var. Mayer' as a synonym, and associates his plant with *J. flaccidus* and *J. stenophyllus*.

Swamps and marshes, generally at low altitudes. Rare on the mountains in the west. More frequent in the summer rain areas.

CAPE, SW.:—TULBAGH: Gt. Winterhoek, *E. P. Phillips* 1697! RIVERSDALE: Riversdale, *Muir* 3030! Kampsche Bay, *Muir* 3480!

CAPE, E.:—GEORGE: George, *Schlechter* 2341! HUMANSDORP: Krom River, Drège 1604, f! PT. ELIZABETH: *Patterson* 3325! ALBANY: Assagaibosch, *Ecklon & Zeyher*! Grahamstown, *Daly & Cherry* 918! SOMERSET: Somerset East, *MacOwan* 1953! BATHURST: Visch River, Drège 1604, c! STOCKENSTROM: Katberg, *Adamson* 306! Hogsback, *Ratray* 396! STUTTERHEIM: Fort Cunyngham, *Schonland* 70! MT. CURRIE: Kokstad, *Mogg* 1641! MT. FLETCHER: Satsama's Pk., *Galpin* 6876, p.pt.! UNLOCALISED: Cape, Drège 1604, i!

NATAL:—DURBAN: Umbilo, *Moss*, 5951, p.pt.! Umtini River, *Schlechter* 5894! UMGENI: Umgeni, *Thode* 5694! P. M. Burg, *Bews* 9! ESTCOUET: Mooi River, *Mogg* 7241! 220, p.pt.! Balgowan. *Mogg* 3861!

BASUTOLAND:—Leribe *Dieterlen* 748, b! 748, p.pt.! 767, p.pt.! *E. P. Phillips*!

TRANSVAAL:—HEIDELBERG: Witpoortje, *Moss* 16558! MIDDELBURG, *Stent* 5261! WAKKERSTROOM: Volksrust, *Mogg* 7531! ERMELo, *Henrici* 1357! CAROLINA: *Moss & Rogers* 1178! LYDENBURG, *Schlechter* 3745!

*Var. sphaerocephalus.*

Marshes or damp soil, especially on sand.

CAPE PROVINCE :—CAPE : Cape Flats, *Moss* 9155! *Adamson* 226! 234! 235! Fishhoek, *Adamson* 257! 258! S. Cape Peninsula, *Adamson* 314! 352! STELLENBOSCH : Stellenbosch, *Adamson* 159! Firgrove, *Adamson* 130! 133! 137! 139! ALBANY : Howiesons Poort, *Rennie* 205! Frame's Drift, *Paterson* 1969! K. WILLIAMS TOWN : *Hilner* 107!

NATAL :—DURBAN : Umbilo, *Moss* 5951, p.pt.!

18. *JUNCUS SUBCUNEATUS*, sp. n.

*Juncus Dregeanus* auct., p.pt.

Perennis, laxe caespitosa. *Folia* plana 3–5 mm. lata, in statu sicco involuta, caulibus dimidio vel ultra breviora. *Caules* teretes in statu sicco distincte sulcati, 10–30 cm. alti. *Inflorescentia* simplex vel umbellata ramis 3–5, 3–5 capitula ferentibus. *Capitula* pedunculata vel sessilia aggregataque, parva, infra cuneata, 5–10 flora. *Bractea* infima (vel duae) frondescens inflorescentiam saepius superans. *Tepala* externa longiora, nigro-aristata; interna obtusa marginibus albo-hyalinis latis involutis. *Stamina* 3–4 vel 6, perianthio duplo breviora. *Antherae* parvae filamentis breviores. *Stylus* brevis sed distinctus tempore anthesis ovario dimidio brevior. *Capsula* perianthio brevior, obovata, superne rotundata, breviter mucronata, nitida castanea vel ferruginea. *Semina* lutea parva rotundato-ovata, distincte apiculata.

*Var. LATIFOLIA*, nov.

Subcaespitosa; *folia* plana; *inflorescentia* umbellata; *capitula* multiflora, pedunculata; *bractea* infima inflorescentiam superans; *flores* majores; *tepala* distincte aristata.

The type is Rogers 21308!

*Var. MINOR*, nov.

Minor, caespitosa; *folia* breviora in statu sicco involuta; *capitula* pauca, pauciflora, congesta vel pedunculata; *flores* minores; *tepala* subaequalia.

The type is Moss 7986!

*J. subcuneatus* is distinguished from *J. Dregeanus* by the small few-flowered heads, which are cuneate below and not hemispherical, the longly aristate perianth, and the short but distinct style. The capsule is also more rounded on top and the seeds distinctly apiculate. The plant is less tufted and has broader and longer leaves. The name of this species and that of the following one were suggested by the late Prof. C. E. Moss, who first distinguished these plants as separate from *J. Dregeanus*.

Marshes and stream-sides generally scattered. *Var. latifolius* occurs in the coastal regions in the south and west, *var. minor* in the eastern regions. On the higher parts of the eastern plateau plants with one head are common.



CAPE, SW. :—STELLENBOSCH : Firgrove, *Adamson* 129! CALEDON : *Hermanus*, *Adamson* 36!

CAPE, E. :—UITENHAGE : Zwartkops River, *Ecklon & Zeyher* 899! *Ecklon & Zeyher* 799! PT. ELIZABETH : Springfields, *Paterson* 3306! ALBANY : Grahams-town, *Hilner* 258! Botha's Valley, *Schonland* 4420! Bushman's River, *Daly* 791! KING WILLIAMS TOWN : Amatola Mts., *Dyer* 318! HERSCHEL : Sterkspruit, *Hepburn* 295!

NATAL :—DURBAN : Clairmont, *Schlechter* 2828! Umtini River, *Schlechter* 5874! UMGENI : P. M. Burg, *Wilms* 2328! ESTCOURT : Mooi River, *Mogg* 220! p.pt., 7200! Balgowan, *Mogg* 5557! LION'S RIVER : Lidgetton, *Mogg* 1367! 1371! 3610! 559!

BASUTOLAND :—Leribe, *Dietelen* 396! Lickhoele, *Dieterlen* 1249!

TRANSVAAL :—JOHANNESBURG : Rosebank, *Moss* 7986! Florida, *Moss* 7922! HEIDELBURG : Witpoortje, *Moss* 2754! CAROLINA, *Rogers* 21308!

#### 19. JUNCUS SUBGLOBOSUS, sp. n.

Dense caespitosa. *Folia* linearia, filiformia, rigida, plana, sed in statu sicco canaliculata involutaque. *Caules* tenues, rigidi, teretes, laeves, 10–20 cm. alti, capitulo terminali unico composito, lobato, sphaerico vel hemisphaerico, saepius asymmetrico, ferentes. *Bractea* infima frondescens, capitulum aequans vel paullo superans. *Flores* parvae, 3–3.5 mm., ferrugineae, castaneae vel etiam nigrescentes. *Tepala* subaequalia; externa mucronata nec non aristata; interna obtusa, sed propter margines albo-hyalinos involutos, acuta videntur. *Stamina* 3 vel 6, perianthio duplo breviora, antheris filamentis brevioribus vel subaequantibus. *Stylus* brevissimus. *Capsula* perianthio paullo brevior, ovata, superne trigona, breviter mucronata, rubro-ferruginea. *Semina* parva, reticulata, ovata, obliquiter apiculata.

Allied to the two preceding species, but readily distinguished by the densely tufted habit and single dense heads; also by the small dark flowers with outer perianth shortly mucronate, the ovate capsule, and obliquely apiculate seeds.

The type is *Moss* 7922 *bis*!

Marshes and stream-sides, in the grassland region of the High Veld.

CAPE PROVINCE :—MT. FLETCHER : Drakensberg, *Galpin* 6876, p.pt.!

BASUTOLAND :—Leribe, *Dieterlen* 748! 4811! 6610!

TRANSVAAL :—JOHANNESBURG : Florida, *Moss* 7922 *bis*! 12054! PRETORIA : Zuickerbosch, *Schlechter* 3502!

20. JUNCUS INDESCRIPTUS Steud. Syn. Pl. Glum. ii, p. 304 (1855); Buchen. p. 479 (1875), p. 442 (1890), p. 253 (1906); Baker, in Flora Cap. vii, p. 26 (1896). *J. capensis* ssp. *parviflorus* Buchen. p. 491 (1875).

Loosely tufted. Flowering stems 20–40 cm. *Leaves* dark green, shining, flat or channelled above, about  $\frac{1}{4}$ – $\frac{1}{2}$  length of stem. *Sheaths* loose without

auricles. *Inflorescence* of 3–20 heads, branches ascending. *Heads* hemispherical, 8–12-flowered, occasionally more (–24). *Flowers* small, 3 mm., dark brown or nearly black. *Perianth* equal; external acute, mucronate; internal obtuse, involute. *Stamens* 6, about  $\frac{3}{4}$  perianth, anthers equalling or slightly exceeding filament. *Style* at least equalling ovary, stigmas long, red, exserted. *Capsule* dark brown, less than or just equalling the perianth, turbinate, obovate, bluntly trigonous, shortly mucronate. *Seeds* brown, ovate, very shortly apiculate.

A distinct species characterized by the ascending rhizome; loosely tufted habit; deep green, channelled leaves without auricles; small dark flowers in dense but not numerous heads; relatively long filaments and the rounded mucronate capsule almost equalling the perianth.

The species was founded on Drège 1604, h, from the Berg River at Paarl. Krauss's specimens from the Zonder Ende River at Swellendam, which Buchenau made the type of subspecies *parviflorus* of *J. capensis*, agree with this species in all essential characters. They differ from Drège's specimens only in having smaller and paler-coloured flowers. The plants certainly belong to *J. indescritus*.

Swamps and marshes, generally in stagnant water and on soils with much organic matter. More common in the eastern regions, but extending along the coast-belt from Natal to Paarl, rare in the interior. The plant extends to tropical Africa.

\* CAPE, SW.:—PAARL: Berg River, Drège 1604, h! Fransshoek, Schlechter 9222! CALEDON: Villiersdorp, Adamson 61! 64! 65! 66! Viljoen's Pass, Adamson 63! SWELLENDAM: Riv. Zonder Einde, Krauss!

CAPE, E.:—BATHURST: Port Alfred, Salisbury! KING WILLIAMS TOWN, Hilner 130! Sim 2850! E. LONDON: East London, Hilner 298! Fort Grey, Adamson 287–8–9! 290–1–2! 296–7–8! KENTANI: Kentani, Pegler 2093! STUTTERHEIM, Schonland 2850! Sim 2548! CATHCART: Toise River, Hilner 372, p.pt.! TRANSKEI, Bennie 413! KOMGHA: Komgha, Flanagan 1006, p.pt.! TEMBULAND: Bashee River, Schlechter 6281 a!

NATAL:—DURBAN: Clairmont, Wood 12038!

TRANSVAAL:—UNLOCALISED, Rehmann 5742!

NYASSALAND:—Stolz-Schlechter 1144!

21. *JUNCUS SONDERLIANUS* Buchen. p. 476, t. x (1875), p. 440 (1890), p. 252 (1906); Baker, in *Flora Cap.* vii, p. 25 (1895). *J. capensis* var. *angustifolius* E. Mey. Syn. Junc. p. 49 (1822), p.pt. *J. capensis* var. *capitatus* Nees, in *Linnaea*, xx, p. 244 (1847) (nomen).

Plant loosely tufted, almost turf-forming. *Rhizomes* ascending, branched. *Stems* short, 5–18 cm. *Leaves* 2–3 mm. broad, flat or slightly channelled above, without auricles, sheaths broad, loose. *Leaves* shorter than stems. *Inflorescence* of few heads, 1–2–6. *Heads* approximated. *Lowest bract* leaf-like,

exceeding inflorescence. *Heads* 6–10-flowered. *Flowers* 4 mm., brown or dark; external perianth exceeding inner, aristate. *Stamens* 6,  $\frac{1}{2}$  length of perianth, anthers equalling filaments. *Style* long. *Capsule*  $\frac{2}{3}$  perianth, ovate, trigonous, apiculate.

The type is Drège *J. capensis* var. *angustifolius*, e!

Damp places on sandy soil at low altitudes and especially near the sea. Confined to the south coastal region between Port Elizabeth and Riversdale.

CAPE PROVINCE :—RIVERSDALE : Muir 3400! KNYSNA : Duthie 879! MOSSEL BAY, Burchell 6237! 6247! PORT ELIZABETH, Drège, *J. cap. angust.*, e! Burchell 4386! CAPE RECEIFE, Ecklon & Zeyher! WALMER, Paterson 2318!

22. *JUNCUS ANONYMUS* Steud. Syn. Pl. Glum. ii, p. 304 (1855) (emend.); Buchen. p. 478 (1875), p. 441 (1890), p. 252 (1906); Baker, in Flora Cap. vii, p. 25 (1895). *J. acutangulus* Buchen. p. 480 (1875), p. 442 (1890), p. 253 (1906); Baker, l.c. p. 26 (1895). *J. capensis* ssp. *longifolius* var. *strictissimus* Buchen. p. 482 (1873), p. 444 (1890), p. 253 (1906), pro parte.

Tufted, but not caespitose. *Stems* firm, up to 80 cm. *Leaves* much shorter than stems, flat or channelled above, 2–3 mm. wide. *Inflorescence* many-headed, branches ascending or erect, firm. *Lowest bract* leaf-like, shorter than or equalling inflorescence. *Heads* many-flowered (8–16), more or less spherical, squarrose in fruit. *Flowers* 4 mm., distinctly 3-angled. *External perianth* aristate, rough on back, exceeding involute, obtuse, hyaline-margined inner. *Stamens* 6,  $\frac{1}{2}$ – $\frac{2}{3}$  perianth. *Anthers* longer than filaments. *Capsule*  $\frac{2}{3}$  perianth, ovate cylindrical, bluntly 3-angled, longly mucronate. *Seeds* relatively large, obliquely obovate, reticulate.

*J. anonymus* is readily distinguished from *J. capensis* by the numerous many-flowered heads becoming squarrose in fruit, the larger flowers, and the firm erect stem, and stiff, short, broad leaves. This species flowers and fruits earlier than *J. capensis*. Where they grow associated the former has fruit by the time the latter opens its flowers.

After an examination of the type-specimens and others I have united *J. anonymus* and *J. acutangulus*. The former was founded on Drège 1604 a from Du Toits Kloof. *J. acutangulus* is based on Zeyher 4318 from 'Somerset, Stellenbosch', and on Ecklon 100 from Wynberg. There does not seem any character that can separate the plants as species or even varieties. Drège 1604 a has less stiff leaves, fewer heads, and longer points to the perianth than Ecklon's or Zeyher's specimens, but other specimens named *J. acutangulus* by Buchenau bridge the gap completely, e.g. Zeyher 100, and another specimen of Ecklon from Wynberg.

The type of Buchenau's var. *strictissimus* of *J. capensis* is Gueinzus from Hottentots Holland. This sheet has two specimens; one is identical with Zeyher 4318, the other has narrower leaves, smaller heads with fewer flowers, and belongs to *J. capensis*. This last is the plant figured by Buchenau (l.c. 1875, t. xi).

Damp places especially on sandy soils. Not in swamps nor by streams. Confined to the south-west Cape region. This species seems less water-demanding than the others in this series.

CAPE PROVINCE :—CAPE : Wynberg, *Ecklon*! Kirstenbosch, *Adamson* 70! 167–8–9–170! 235! 237–8–9! Table Mt., *Adamson* 274! STELLENBOSCH : Stellenbosch, *Adamson* 156! Somerset West, *Zeyher* 4318! Hottentots Holland, *Gueinzius*, p.pt.! WORCESTER : Du Toits Kloof, *Drège* 1604 a! UNLOCALISED : Cape, *Ecklon & Zeyher* 100! *J. capensis capitata* 1, 2, *Ecklon*! *Wallich*!

### 23. JUNCUS APICULATUS, sp. n.

*Juncus capensis* ssp. *geniculatus* Buchen. p. 492, t. xi (1875), p. 446 (1890), p. 255 (1906) (non *J. geniculatus* Schrank, Baier. Fl. i, p. 613 (1789).

Affinis *J. capense* sed differt caulibus altioribus 30–70 cm. ; *caulibus* folisque subflaccidis ; *foliis* planis usque ad 3–4 mm. latis sine auriculis ; *inflorescentia* multicapitata ramis divaricatis ; *floribus* pallidis ; *staminibus* 6, antheris filamenta aequalibus ; *capsula* perianthio vix brevior, apice apiculata vel brevissime mucronata.

A plant easily distinguished in fruit by the longer apiculate capsule. The rather broad leaves and divaricate inflorescence are also characteristic. The inflorescence often shows proliferation and formation of vegetative buds.

Buchenau founded *geniculatus* as a subspecies on MacOwan 2020 and 2019. These two plants are, however, not identical ; 2020 agrees with the descriptions completely, whereas 2019 shows marked divergencies. The latter agrees exactly with *Drège* 1604 e, from Grahamstown, which is the type of *J. capensis* var. *delicatulus*. In raising the plant to specific rank a new name was required, owing to the existence of *J. geniculatus* Schrank, which is a different plant.

Swamps and margins of rivers with permanent water. Rather rare.

CAPE PROVINCE :—ALBANY : Howieson's Poort, *MacOwan* 2020! 3678! E. LONDON : *Rattray* 730! KENTANI : *Pegler* 1107!

24. JUNCUS CAPENSIS Thunb. Prodr. Pl. Cap. p. 66 (1794) (emend.) ; Buchen. p. 482 (1875), p. 443 (1890), p. 253 (1906) ; Baker, in Flora Cap. vii, p. 26 (1895).

Very variable in size, densely tufted. *Leaves* narrow, linear, often appearing subulate, bending downwards. *Stems* slender, often inclined, exceeding leaves. *Inflorescence* many-headed, branches ascending, slender. *Flowers* 3–4 mm., outer perianth longer, mucronate. *Stamens* 6, about  $\frac{2}{3}$  perianth, anthers much longer than filaments. *Style* long, stigmas exserted. *Capsule* shorter than perianth, c.  $\frac{2}{3}$ , trigonous, distinctly mucronate or rostrate.

Var. *ECKLONII* Buchen. p. 485 (1875) (emend.). *J. capensis* ssp. *longifolius* E. Mey, var. *gracilior* Buchen. p. 483 (1875), p.pt. *J. capensis* ssp. *angustifolius* E. Mey. var. *Ecklonii*, Buchen. p. 485. *J. stenophyllus* Steud. Syn. Pl. Glum. ii, p. 303 (1855). *J. flaccidus* Steud. l.c. 303.

Stems 15–30 cm. *Leaves* slender. *Inflorescence* ascending or subumbellate with firm branches. *Heads* few to many, typically few-flowered, 1–8. *Flowers* small, 3–4 mm. *Perianth* firm.

The type is Ecklon 897!

Var. *DELICATULUS* Buchen. p. 490 (1875) (pro subsp.). *J. delicatulus* Steud. l.c. 304.

Slender, *leaves* very slender, much shorter than stem. *Inflorescence* branches slender, erecto-patent. *Heads* regularly cymose, many-flowered. *Flowers* small, 3–3.5 mm., pale. *Perianth* thin, submembranous.

The type is Drège 1604 e!

Var. *MACRANTHUS*, nov.

*Juncus capensis* ssp. *longifolius* E. M. var. *gracilior* Buchen. p. 483, p.pt. ; et var. *strictissimus* Buchen. p. 482, p.pt. *J. cymosus* Spreng. Neu Entdeck. ii, p. 105 (1821), non Lamk., fide Buchen.

Robustior. *Caules* 30–40 cm. alti. *Inflorescentia* multicapitata, ramis ascendentibus, capitula multiflora c. 12–20. *Flores* majores 4–4.5 mm.

The type is Adamson 88! 89!

Damp places at low altitudes ; stream-sides and margins of swamps also around temporary vleis. On mountains ascends to about 2,000 feet. Rare on sandy flats. South or south-western coastal districts.

Var. *Ecklonii*.

CAPE PROVINCE :—CAPE : Cape Town, *Ecklon* 35! 897! *Burchell* 8! 253! 471! Table Mt., *Ecklon & Zeyher* 85! *E. Meyer* 22! *Ecklon* 897! 898! *Moss* 7924! *W. Dod* 2389! *Adamson* 108! 109! 273! Kirstenbosch, *W. Dod* 3432! *Adamson* 110! 192! 242! 246! 248! 250! Claremont, *W. Dod* 3653! Hout Bay, *Adamson* 93! 99! Camp's Bay, *Burchell* 852! *Adamson* 74! 76! 80! 94! 95–6–7–8! 100! 105–6–7! Kommetje, *Adamson* 81! 101–2–3–4! 283! 304! Kalk Bay, *Moss* 7925! Sea Point, *W. Dod* 3527! 3328! Constanza, *W. Dod* 2366! Cape Flats, *Rehmann* 1820! *Moss* 5619! STELLENBOSCH : Stellenbosch, 999 in *Mus. Alb.*! Sir Lowry Pass, *Kunze* 94! CALEDON : Grabouw, *Ecklon* 45! *Meyer* 9! TULBAGH, *Meyer* 12! WORCESTER, *Ecklon & Zeyher* 1, 11! ; & 1, 12! *Zeyher*! Bains Kloof, *Schlechter* 9176! RIVERSDALE : Riversdale, *Muir* 302! 3026! 3387! 3480! *Schlechter* 1935! SWELLENBOSCH : Riv. Zonder Einde, *Thorne*! Swellendam, *Adamson* 326! Zuurbraak, *Adamson* 304! GEORGE : George, *Zeyher* 4317! KNYSNA : Knysna, *Bolus* 2497! *Schlechter* 5950! 5957! *Schotland* 3576! *J. Phillips* 3–4! 14! *Fourcade* 2447! PT. ELIZABETH : Springfields, *Paterson* 3294! ALBANY : Grahamstown, *Hilner* 261! *Daly & Sole* 547! *Daly & Cherry* 917! *Bennie* 635! Howieson's Poort, *Dyer* 1729! *Britten* 978! Assagabosch, *Burchell* 4175! Trapp's Hill, *Daly* 196! SOMERSET : Boschberg, *MacOwan* 1744! UNLOCALISED : *Meyer* 15! *Ecklon*! *Harvey* 3584! *Penther* 873! *Zeyher* 443! 4315! 4316! Drège, *J. cap. angust.*, b!

*Var. delicatulus.*

CAPE PROVINCE :—CAPE : Table Mt., *Meyer* 21! CALEDON : Palmiet River, *Meyer* 19! *Ecklon* 35! *Bolus* 4218! WORCESTER : Bain's Kloof, *Rehmann* 2307! SWELLENDAM, 16. *Ecklon & Zeyher* 91! KNYSNA : Knysna, *Duthie* 930! 966! UITTENHAGE : Zwartkops River, *Drège* 1604 d! Van Stadens, *Paterson* 2677! ALBANY : Grahamstown, *Rennie* 201! *Drège* 1604 e! *Daly & Cherry* 971! *Britten* 930! *Rogers* 27508! Howieson's Poort, *MacOwan* 2019! *Schonland* 660! STOCKENSTROM : Hogsback, *Ratray* 397!

*Var. macranthus.*

CAPE PROVINCE :—CAPE : Cape Town, *N. J. Andersson*! Kirstenbosch, *Moss* 10138! *Adamson* 243! 245! 248! Rondebosch, *Bolus* 4859! *Adamson* 256! Tokai, *W. Dod* 1957! Kalk Bay, *Adamson* 190! Camp's Bay, *Adamson* 73! 77! *Thoday*! Kommetje, *Adamson* 71! 72! 78! 83! 84! 85! 86! 87! 88! 89! 90! 91! 92! 269! Cape Flats, *Adamson* 262! *Guthrie* 1386! STELLENBOSCH : Stellenbosch, *Adamson* 161! CALEDON : Mossel River, *Potts* 1569! Grabouw, *Bolus* 4220! RIVERSDALE : Albertinia, *Muir* 2554!

UNLOCALISED, *Meyer* 23! *Kunze*! *Drège* 1604 k!

In the determination of Thunberg's species, which is so poorly diagnosed that it is indeterminable in the absence of specimens, Buchenau (1875) has been followed and the name *J. capensis* retained for this exceedingly common plant of the south-west. The species has been narrowed by the separation of some of the plants previously included. Buchenau recognised five subspecies, two of which were further subdivided. Of the subspecies one is now raised to specific rank and one transferred to *J. indescriptus* (q.v.).

Of the varieties recognised by Buchenau, var. *strictissimus* has been treated under *J. anonymus*, q.v. The var. *gracilior* was founded on a plant of Bergius! The various plants placed by Buchenau under this variety are divided between large-flowered, strong, tall plants and smaller-flowered plants indistinguishable from var. *Ecklonii*. The name *gracilior* has been dropped therefore as liable to cause confusion. The var. *flaccidus* was also founded on plants collected by Bergius. I have not seen the type, but a large number of other specimens have been examined, many of which were named by Buchenau. All these seem to be from moist shady places, or immature. Except for characters most probably due to habitat, these plants agree with var. *Ecklonii* as here defined, and are sunk therein. The present limitation of *J. capensis* makes an easily recognised and well-defined species which, though variable with habitat, retains all essential features.

25. *JUNCUS SPHAGNETORUM*, sp. n.

*Juncus capensis* ssp. *angustifolius* E. Mey. var. *sphagnetorum* Buchen. p. 489, t. xi (1875) (bad), p. 445 (1890), p. 254 (1906).

Affinis *J. capense*, differt *rhizomati* erecto vel obliquo ramoso; *foliis* brevibus caulium dimidium aequantibus; *inflorescentia* pauci-capitata 1-7, capitulis

parvis paucifloris (2-7); *floribus* parvis 2-3 mm., pallidis vel ferrugineis; *staminis* dimidium perianthii aequantibus, antheris filamentis paullo longioribus; *capsula* perianthi vix brevior, pallide ferruginea.

Differs from *J. capensis* in growth-habit; the short stiff leaves; small flowers in few heads, and the longer mucronate fruit. The plant is almost turf-forming, not caespitose. The name '*sphagnetorum*' applied by Buchenau is not especially suitable; the plant most commonly grows on sand or gravel.

The type is Drège *J. capensis* v. *angustifolius*, c.

Permanently damp places on shallow soils on mountains. Generally on gravel or sand, but also on peat or *Sphagnum*. Confined to the south-western Cape.

CAPE, S.W. :—Table Mt., Drège, *J. cap. angust.*, aa! Rehmann 611! Compton! Du Toits Kloof, Drège, *J. cap. angust.*, c & cc! Worcester Mts., Rogers 17363! 17349! Swartberg Pass, Adamson 303! Meirings Poort, Adamson 183! 184! 185!

26. *JUNCUS SINGULARIS* Steud. Syn. Pl. Glum. ii, p. 302 (1855); Buchen. p. 438, t. ix. (1875), p. 408 (1890), p. 237, fig. 123 (1906); Baker, in Fl. Cap. vii, p. 25 (1895).

Tufted, stems 10-15 cm. *Leaves* all basal, distichous, unifacial, laterally compressed, not septate, minutely channelled above. *Stems* exceeding leaves. *Inflorescence* umbellate, branches ascending. *Heads* many-flowered (7-9-15). *Lowest bract* leaf-like, shorter than inflorescence. *Flowers* 4 mm.; outer perianth long aristate; inner involute with broad membranous margins. *Stamens* 6, shorter than perianth, anthers longer than filaments. *Style* long. *Capsule* shorter than perianth, ovate, 3-angled, long mucronate, shining. *Seeds* small, apiculate.

This species is known only from the collections of Drège from 'between Bethelsdorp and van Stadensberg' (Drège 1604 b).

*J. singularis* is very closely allied to the following species (*J. atropurpureus*), from which it differs in the unifacial almost distichous leaves.

Buchenau (p. 438 (1875)) made this species the type of a separate subgenus '*Junci singulares*' based on the character and arrangement of the leaves. As the plant in all other features agrees with the '*Junci graminifolii*' it is placed there, as was done by Vierhapper in Engler and Prantl, Auf. 2, 15 a, p. 216 (1930).

## 27. *JUNCUS ATROPURPUREUS*, sp. n.

*Juncus capensis* s.sp. *longifolius* E. Mey. var. *strictissimus* Buchen. p. 482 (1875), p.pt.; p. 253 (1906), p.pt.

Laxe caespitosa. *Rhizoma* breve, erectum vel obliquum. *Caules* 20-30 cm. alti. *Folia* erecta, viridia, nitida, superne canaliculata. *Vaginae* laxae in auriculos duos parvos in foliis ultimis productae. *Caules* foliis duplo longiores. *Inflorescentia* umbellata, ramis erectis vel erecto-patentibus, multicapitata. *Capitula* 6-12, segregata vel plus minusve aggregata, multiflora (5-15), hemisphaerica. *Bractea infima* frondescens, inflorescentia brevior vel fere aequans.

*Bracteae* florum membranaceae, nigro-aristatae. *Flores* 4–5 mm. longae. *Tepala* externa distincte longiore, nigro-aristata; interna obtusa, involuta, omnia albo-marginata, intus atro-purpurea, extra pallida vel viridia. *Stamina* 6, perianthio dimidio breviora. *Antherae* filamentis triplo longiores. *Stylus* longus, stigmata exserta. *Capsula* perianthio brevior obovata longe mucronata. *Semina* apiculata.

This plant is distinguished from the others in this group by its dark green channelled leaves, large flowers in hemispherical heads, and the white-margined perianth, deep purple internally.

The type is Adamson 171.

Damp hollows with black sandy soil especially near the sea and where liable to short submergence in winter. Found only on the Cape Flats:—Near Lakeside, Adamson 171–2–3! 193! Muizenberg, Adamson 176! 177! Moss 7933! Zeekoe Vlei, Adamson 232! Cape Flats, Rehmann 1819! Sarepta, Acock!

Buchenau refers Rehmann 1819 to his var. *strictissimus* of *J. capensis* (p. 254 (1906)). The plant undoubtedly belongs to this species and is quite distinct from the other specimens referred to the variety.

## B. ANNUAL SPECIES.

### *Key to the annual species.*

1. Stamens 3. Head 1 often pseudolateral. External perianth longer ..... (28) *J. capitatus*.  
     Stamens 6. Heads 1 or several. Inflorescence terminal .... 2.
2. Heads many-flowered, 6 or more ..... 3.  
     Heads few-flowered, 1–5 ..... 7.
3. Perianth equal or external longer ..... 4.  
     Internal perianth distinctly longer ..... (30) *J. inaequalis*.
4. Style long ..... 5.  
     Style very short or none ..... (37) *J. diaphanus*.
5. Internal perianth obtuse, involute ..... 6.  
     Internal perianth acute. Heads spherical, squarrose ..... (31) *J. Sprengelii*.
6. Flowers large, pale. Capsule blunt. Plant stiff, glaucous .. (36) *J. scabriusculus*.  
     Flowers dark or black. Leaves flat. Capsule mucronate .. (29) *J. cephalotes*.
7. External perianth distinctly shorter than inner. Flowers pale ..... 8.  
     Perianth equal or external longer. Flowers dark ..... 9.
8. Very small. Head 1. Flowers small. Capsule long, mucronate ..... (33) *J. parvulus*.  
     Taller. 3 heads. Flowers large. Perianth with dark spots at tip ..... (32) *J. pictus*.
9. Inflorescence of 1 or few heads ..... 10.  
     Inflorescence of many few-flowered heads ..... 11.
10. Head 1. Capsule, rounded apiculate. Plant very slender .. (34) *J. polytrichus*.  
     Heads 1–5. Capsule distinctly mucronate. Tufted, red .... (35) *J. filifolius*.
11. Style very short or none. Flowers small, brown ..... (38) *J. rupestris*.  
     Style long. Stigmas exserted ..... 12. [Schlechteri.
12. Leaves filiform. Inflorescence cymose ..... (38 b) *J. rupestris* var.  
     Leaves wider. Inflorescence umbellate ..... (39) *J. umbellatus*.



28. *JUNCUS CAPITATUS* Weig. Obs. Bot. xiv, p. 28 (1772) ; Kunth, Enum. Pl. iii, p. 346 (1841) ; Buchen. p. 450 (1890), p. 256 (1906) ; Baker, in Flora Trop. Afr. viii, p. 95 (1901). *J. gracilis* Roth. Bot. Abh. p. 46 (1787), non B. Br., nec Sm. *J. tenellus* Geuns, Pl. Belg. Conf. Indig. Spicil. iv, p. 18 (1823). *J. mutabilis* Cav. Ic. et Disc. Pl. iii, p. 49 (1794). *J. triandrus* Gouan. Herb. Env. Montp. p. 25 (1796).

1-7 cm., often reddish brown. *Leaves* filiform, shorter than stems. *Stems* erect, one-headed. *Heads* pseudolateral, 3-6-8-flowered. Lowest bract leaf-like, exceeding head. *Flowers* 3-3.5 mm., pale. *External perianth* aristate, longer than acute inner. *Stamens* 3,  $\frac{1}{2}$  outer perianth, anthers less than filament. *Capsule* shorter than perianth, red-brown, ovate, mucronate.

Confined to High Veld.

BASUTOLAND :—Leribe, Dieterlen 806 !

TRANSVAAL :—Pretoria, Moss 11949 !

Southern and central Europe, Canary Islands, Azores, N. Africa, Mt. Cameroon, Australia, Newfoundland.

29. *JUNCUS CEPHALOTES* Thunb. Prod. Pl. Cap. p. 66 (1794) (emend.) ; Willden. Linn. Sp. Pl. ii, p. 215 (1799), p.pt. ; Persoon, Syn. Pl. i, p. 385 (1805), p.pt. ; Buchen. p. 451, t. vii (1875), p. 454 (1890), p. 259 (1906) ; Baker, in Flora Cap. vii, p. 24 (1895). *J. capensis* var. *angustifolius* E. Mey. Syn. Junc. p. 48 (1822), p.pt., *vide* Buchen. *J. cephalotes* var. *minimus* Hochst. Flora, xxviii, p. 342 (1845), p.pt. *J. isolepoides* Nees, in Linnaea, xx, p. 244 (1847), p.pt. (nomen).

3-12 cm. high. *Leaves* flat, up to 3 mm. wide, shorter than stem. *Inflorescence* branches with 1-2 heads. *Heads* 1-5(-8), 6-12-flowered, occasionally, 8-20, hemispherical. *Bract* white, membranous, lowest occasionally with short leafy blade. *Flowers* dark brown or black, perianth equal or external longer ; external aristate, rough on back ; internal involute. *Stamens* 6, shorter than perianth, anthers elongate, filaments at anthesis very short, but becoming equal to anthers. *Style* long, stigmas red, exserted. *Capsule* shorter than perianth, rounded ovate, shining, mucronate. *Seeds* reticulate.

Var. *USTULATUS* Buchen. p. 451 (1875).

*Leaves* flat, broad. *Heads* hemispherical, many-flowered. *Flowers* 3.5-4 mm. ; external perianth about equalling internal.

The type is Ecklon 13.

Var. *VARIUS* Buchen. p. 451 (1875).

*Leaves* narrow. *Heads* smaller, often nearly spherical. *Flowers* 3-3.5 mm. ; usually brown not black as in var. *ustulatus* ; external perianth distinctly longer.

The type is Ecklon from Camps Bay !

Damp places, especially on sandy soils. Very common in the south-west, but apparently rare or absent elsewhere. The two varieties occur together, the var. *ustulatus* being much more common.

CAPE PROVINCE :—PIQUETBERG, *Bolus* 13660, p.pt.! MALMESBURY : Malmesbury, *Schlechter* 1612! CAPE : Table Mt., *Ecklon* 901! *Ecklon*! Camp Ground, *W. Dod* 3479! *Adamson* 199! Rondebosch, *Adamson* 207-8-9-10-11! 202-3! 225! 323! Wynberg, *Schlechter* 1573! Simons Bay, *Wright*! Fishhoek, *Adamson* 52-3-4-5! 57-8-9! 60! 113! 114! 320! Witsands, *Adamson* 44! Kommetje, *Adamson* 228! 230! Smitswinkel Bay, *Adamson* 43! Maitland, *W. Dod* 3249! STELLENBOSCH : Stellenbosch, *Krauss*! *Duthie* 109! 1150! 1156 a! PAARL : Klein Drakenstein, *Drège*, bb! Berg River, Wellington, *Adamson* 315! Wemmershoek, *Adamson* 50! Franshoek, *E. P. Phillips*! CALEDON : Houwhoek, *Penther* 365! Onrust, *Adamson* 47! 48! 49! 112! PT. ELIZABETH, *Paterson* 2318! UNLOCALISED, *C. B. S. Harvey* 355! *Zeyher* 13! 4320!

Var. *varius*.

CAPE : Camps Bay, *Ecklon*! *Zeyher* 355! *Ecklon & Zeyher*! Red Hill, *Adamson* 350!

Rather than upset the accepted nomenclature I have followed Buchenau in his argument for the retention of Thunberg's name for this common annual plant of the south-western Cape region.

30. *JUNCUS INAEQUALIS* Buchen. p. 455 (1875), p. 455 (1890), p. 260 (1906) ; Baker, in *Flora Cap.* vii, p. 24 (1895). *J. isolepoides* Nees, in *Linnaea*, xx, p. 244 (1847), p.pt. (nomen).

Variable in size, 3-30 cm. Leaves flat, 2-3 mm. broad, shorter than stems. Stems erect, stiff. Inflorescence 1-15 heads, branches ascending. Heads 6-20-flowered. Flowers 3-5 mm.; external perianth shorter than internal, acute, mucronate, or shortly aristate; internal obtuse, with involute membranous margins. Stamens 6, shorter than inner perianth, anthers equally or shorter than filaments. Style long, stigmas exserted. Capsule shorter than perianth, ovate, trigonous, mucronate. Seeds ovoid, very shortly apiculate.

Var. *GENUINUS* Buchen. p. 455, 7, t. vii (1875), emend. incl. var. *viridescens* Buchen.

15 cm. high or more. Inflorescence many-headed, umbellate or cymose. Heads small, few-flowered, 6-10. Flowers c. 3 mm. Anthers equalling filaments.

The type is *Ecklon* 24!

Var. *SQUARROSUS*, nov.

Minor, saepius minus 12 cm. alta. Folia breviora. Capitula pauca, 1-5, majora, sphaerica, ultimo squarrosa. Flores 4-5 mm. longae. Antherae filamentis breviores.

The type is *Schlechter* 10608!

Var. *ALTUS*, nov. *J. altus* Buchen. p. 457 (1875), p. 456 (1890), p. 260 (1906); Baker, in *Flora Cap.* vii, p. 24 (1895).

Taller 20–40 cm. *Leaves* broader. *Inflorescence* many-headed, umbellate. *Heads* spherical, large. A larger, stronger-growing plant in all features.

The type is Ecklon and Zeyher from Kogman's Kloof!

After examination of the type-specimens I cannot separate Buchenau's two varieties, *genuinus* and *viridescens*, on any character except colour. *J. altus* differs from *J. inaequalis* only in size, and cannot stand as a separate species.

Frequently associated with *J. cephalotes*, but easily distinguished by the stiffer stems and the perianth. It flowers two to three weeks later than *J. cephalotes*.

Damp places especially on sandy soil in the south-western coastal region.

Var. *squarrosus* is the commonest of the three varieties of the species.

Var. *genuinus*.

CAPE PROVINCE:—CLANWILLIAM: Oliphants River, *Adamson* 31! CAPE: Camps Bay, *Ecklon* 24! Rondebosch, *Adamson* 334! Witsands, *Adamson* 111! 267! STELLENBOSCH, *Zeyher* 4319! 4320! *Ecklon* 12! *Adamson* 157! 162! 163! Firgrove, *Adamson* 134! 135! 138! 141! Hottentots Holland, *Gueinzius*! *Zeyher* 46, p.pt.!

Var. *squarrosus*.

CAPE PROVINCE:—PIQUETBERG: Pickeneers Kloof, *Pearson* 5233! *Bolus* 13660, p.pt.! MALMESBURY: Saron, *Schlechter* 10608! CAPE: Kommetje, *Adamson* 341! 343! 346! Cape Flats, *Rehmann* 1823! *Adamson* 199 a! 200! 204! 223! 224! 332! 333! 334! 335! STELLENBOSCH: Firgrove, *Adamson* 132! 160! PAARL: Wellington, *Adamson* 313! 316! 318! 319! CALEDON: Onrust, *Adamson* 45! RIVERSDALE: Riversdale, *Schlechter* 1723!

Var. *altus*.

SWELLENDAM: Kogman's Kloof, *Ecklon & Zeyher*! *Zeyher* 15!

*Juncus cephalotes* × *inaequalis*.

Some plants from sandy soil from near Cape Town are tentatively referred to this hybrid. The habit and appearance approach *J. cephalotes*, but the external perianth, which is rough and aristate, is much shorter than the inner. The stamens are longer than the external perianth, with anthers exceeding the perianth. The capsule is very shortly mucronate and the seeds shortly apiculate. Found growing with undoubted examples of the supposed parents.

Rondebosch, *Adamson* 207!

31. *JUNCUS SPRENGELII* Nees, in *Linnaea*, xx, p. 244 (1847) (nomen); Buchen. p. 449, t. x (1875), p. 453 (1890), p. 259 (1906); Baker, in *Flora Cap.* vii, p. 24 (1895).

Generally small, 3–12 cm. *Leaves* 1.5 mm. broad, flat, shorter than stems, red below. *Inflorescence* 1–3 heads, lowest bract leaf-like, often spreading hori-

zonally. *Heads* 8–15-flowered, spherical. *Flowers* 4–5 mm., squarrose, yellow-brown. *Perianth* about equal; external acuminate, aristate; internal acute, almost aristate. *Stamens* 6,  $\frac{1}{2}$  perianth, anthers longer than filaments. *Style* long, capsule shorter than perianth, pale brown, ovate, triquetrous, gradually narrowed to mucronate point. *Seeds* apiculate.

Easily recognised by the spherical heads and flowers with equal perianth, the inner acute. In appearance it comes nearest to *J. inaequalis* var. *squarrosus*, but is readily distinguished by the perianth. The plants are often confounded in herbaria.

The type is Zeyher 11!

Damp sandy places on mountain slopes. SW. Cape region, rare.

CAPE PROVINCE :—CAPE : Camp's Bay, *Ecklon & Zeyher*! TULBAGH : Waterfall, *Zeyher* 11! WORCESTER : Bains Kloof, *Schlechter* 9129! *Ecklon & Zeyher*!

32. *JUNCUS PICTUS* Steud. Syn. Pl. Glum. ii, p. 305 (1855); Buchen. p. 458, t. vi (1875), p. 457 (1890), p. 260 (1906); Baker, in Flora Cap. vii, p. 23 (1895).

Slender, 10 cm. high. *Leaves* narrow, much shorter than stem. *Inflorescence* with 3 heads each 6-flowered. *Flowers* large (c. 5 mm.), pale; external perianth much shorter than inner, each with a dark spot at tip 'Capsule exceeding perianth' (*Buchenau*).

Known only from Drège's specimens (2742 a) collected at Leliefontein, Kamiesberg, Namaqualand, in 1830.

33. *JUNCUS PARVULUS* E. Mey. & Buchen. in Buchen. p. 447, t. vi (1875); Buchen. p. 458 (1890), p. 261 (1906); Baker, in Flora Cap. vii, p. 22 (1895).

Very small, 2–3 cm. *Leaves* linear, setaceous. *Stems* with one head with 1–3 flowers. *Flowers* small (2.5 mm.), pale; internal perianth distinctly longer, obtuse; external acute, mucronate, both white or greenish with dark midrib. *Stamens* 6, shorter than inner perianth. *Anthers* shorter than filaments. *Capsule* almost equalling perianth, longly mucronate.

Known only from specimens collected by Drège (2472 b) at Modderfontein in 1830.

34. *JUNCUS POLYTRICHUS* E. Mey. & Buchen. in Buchen. p. 448, t. vi (1875); Buchen. p. 459 (1890), p. 261 (1906); Baker, in Fl. Cap. vii, p. 23 (1895)

Very slender, stems filiform, 7–10 cm. *Leaves* flat,  $\frac{1}{2}$  length of stem. *Head* 1, with 1–3 flowers. *Flowers* c. 3.5 mm., brown; external perianth lanceolate, acute, shorter than involute obtuse inner. *Stamens* shorter than perianth, anthers much longer than filament. *Capsule* round ovate, apiculate, shorter than perianth.

Known only from specimens collected by Drège (2472 aa) at Leliefontein in Namaqualand.

35. *JUNCUS FILIFOLIUS*, sp. n.

Planta gracilis 2–10 cm. alta. *Caules* foliaque subglauca infra purpurea. *Folia* linearia, involuta, setacea, caulibus dimidio breviora. *Capitula* pauca, 1–5, raro 7. *Rami inflorescentiae* erecti vel patentes. *Capitula* pauciflora, 2–7, rarissime 9–10. *Bractae* omnes hypsophyllinae. *Flores* 3–4 mm. stramineae, apice purpureae vel castaneae. *Tepala* aequalia vel interna paullo longiora; externa acuta, mucronata, vel aristata; interna plana, obtusa, marginibus latis hyalinis. *Stamina* 6, perianthio breviora, antherae filamentis multo longiores. *Stylus* longus, purpureus, stigmata purpurea exserta. *Capsula* perianthio paullo brevior vel aequans, rubro-castanea, nitida, ovato-trigona, apice distincte mucronata. *Semina* lutea, obovata, brevissime apiculata.

This distinct plant is allied to *J. polytrichus*, from which it differs in the branched inflorescence, more numerous and larger flowers, almost equal perianth, and mucronate capsule almost equalling the perianth.

The type is Adamson 212.

Damp spots liable to flooding on silt, or soil with much organic matter. Found only on Cape Peninsula and Cape Flats.

CAPE PROVINCE :—CAPE : Cape Flats, temporary Vleis, Adamson 25! 26! 27! 143–4–5–6–7! 151–2! 212! 213! 214! 215! 218! 219! 220! S. Peninsula, Adamson 28! 29! 30! 349!

36. *JUNCUS SCABRIUSCULUS* Kunth, Enum. Pl. iii, p. 354 (1841); Buchen. p. 444, t. vi (1875), p. 475 (1890), p. 260 (1906), Baker, in Flor. Cap. vii, p. 22 (1895). *J. subglandulosus* Steud. Syn. Pl. Glum. ii, p. 303 (1855); Buchen. p. 459, t. vi (1875).

Generally small, 2–15 cm., occasionally 25 cm., stiff, glaucous, stem and leaves red below. *Stems* often rough and glandular above. *Leaves* linear, erect,  $\frac{1}{2}$  stem. *Inflorescence* 1–2–5 heads, branches stiff, erect or divaricate. *Heads* 2–20-flowered. *Lowest bract* leaf-like where many heads. *Flowers* up to 5–6 mm., yellow-brown. *Perianth* equal, rather thin; external narrow lanceolate, acuminate; inner broader, involute. *Stamens* 6,  $\frac{1}{2}$  length of perianth, anthers much longer than filaments. *Capsule* slightly less than perianth, red-brown, trigonous, cylindrical, blunt or retuse, very shortly apiculate.

A very distinct species, though exceedingly variable in size and in the number of heads and flowers. In herbaria the plant is confounded with *J. bufonius* or mixed with that species, e.g., Zeyher 4968 and Drège 8790.

Both *J. scabriusculus* and *J. subglandulosus* were founded on Drège 8795. The differences between them are entirely matters of age and situation. Specimens referable to both can be found on the same tuft. The form separated as *J. subglandulosus* Steud. is the commoner, but the other name has priority.

Damp places, especially near the sea. Confined to the south part of the west coast.

CAPE PROVINCE :—PIQUETBERG, *Drège* 8795! CAPE : Cape Town, *Drège* 8790, p.pt.! *Bolus* 4812! Rondebosch, *Adamson* 149! 205! 206! Claremont, *Schlechter* 1673, p.pt.! Witsands, *Adamson* 37! 38! 40! 331! Cape Flats, *Zeyher* 4968, p.pt.! *Adamson* 219! 213! *Rehmann* 1823! Paarden Island, *W. Dod* 3150! Blaauwberg, *Adamson* 39! 41!

37. *JUNCUS DIAPHANUS* Buchen. p. 442, t. vii (1875), p. 460 (1890), p. 262 (1906); *Baker*, in *Flor. Cap.* vii, p. 221 (1895).

Whole plant pale, 28 cm. high, branching from base. *Stems* smooth. *Leaves* shorter than stem, flat, 6 mm. wide. *Heads* 3–4, each 8–15-flowered. *Lowest bract* leaf-like, short. *Flowers* c. 4 mm. *Perianth* pale, diaphanous, with broad memb. margins; external acute; internal of equal length, obtuse. *Stamens*  $\frac{1}{2}$  perianth, anthers shorter than filaments. *Style* short. *Capsule* shorter than perianth, ovate, prismatic, obtuse, mucicous, pale, thin.

This plant is known only from the specimen collected by *Bolus* 188\*, which is labelled 'Albany. Is this the immature state of 188? Leg. *Bolus*'.

38. *JUNCUS RUPESTRIS* Kunth, Enum. Pl. iii, p. 342 (1841); Buchen. p. 441 (1875), p. 460 (1890), p. 261, fig. 121 (1906); *Baker*, in *Flor. Cap.* vii, p. 21 (1895). *J. capensis* var. *minimus* Hochst. *Flora*, p. 342 (1845), p.pt.

Slender, up to 18 cm. *Stems* almost filiform. *Leaves* very short,  $\frac{1}{3}$  of stem. *Inflorescence* with cymose branching. *Heads* 2–6 or more, few-flowered (1–5). *Lowest bract* with small blade, others membranous. *Flowers* small, 2.5–3 mm., brown. *Perianth* equal, or internal slightly longer; external acute, shortly mucronate; internal obtuse, involute. *Stamens* 6, about  $\frac{1}{2}$  perianth, anthers equalling filaments. *Style* very short or none. *Capsule* almost equalling perianth, round-ovate, apiculate. The whole plant usually appears brown.

The type is *Drège* 2471!

Var. *SCHLECHTERI* (Buchen.), comb. nov.

*Juncus Schlechteri* Buchen. in *Engl. Bot. Jahrb.* xxiv, p. 459 (1898), p. 262 (1906).

Differs from type in having bracts and external perianth black aristate, long style with exserted stigmas, and stamens with very short filaments, one-third or less than anthers.

Damp sandy places in W. and SW. Cape.

CAPE PROVINCE :—NAMAQUALAND : Kamiesberg, *Drège* 2471 a! 2471 c! 2471 d! CAPE : Camps Bay, *Ecklon & Zeyher*! Fishhoek, *W. Dod* 3400! *Levy*ns! Simons Bay, *Wright* 527! S. Peninsula, *Adamson* 347! 351! PAARL : Franschhoek, *Schlechter* 9224! 9227! STELLENBOSCH : Stellenbosch, *Duthie* 1731! *Adamson* 164!

\* *Bolus* 188 from Sundays River, Graaf Reinet, is *J. exsertus* Buchen.

## Var. SCHLECHTERI.

CAPE PROVINCE :—WORCESTER : Bain's Kloof, *Schlechter* 9154 !

In reducing *J. Schlechteri* Buchen. to a variety of *J. rupestris* Kunth I have been influenced by the very great similarity between the plants and by the fact that some of the specimens issued under the number of the type of *J. Schlechteri* are wholly or partly *J. rupestris*, e.g., *Schlechter* 9154 in Nat. Herb. Pretoria.

## 39. JUNCUS UMBELLATUS, sp. n.

Annua. *Caules* solitarii vel subcaespitosi usque ad 12 cm. alti. *Folia* basilaria plana superne leviter carinata, in statu sicco involuta, vaginis saepius purpureis, caulibus breviora. *Inflorescentia* umbelliformis, capitulis 1–3-floris, longe pedunculatis, numerosis, in apice caulium dispositis. *Bractae infimae* duae frondescentes, inflorescentia breviores, vel subaequantes. *Bractae* florum aristatae, floribus breviores. *Flores* parvae, 2–2·5 mm., rubro-castaneae vel rarius pallidae; tepala externa distincte longiora, aristata, marginibus membranaceis; interna obtusa, involuta, medio viridia, latero lineis castaneis picta. *Stamina* 6, tepalis multo breviora, antheris filamentis triplo longioribus. *Stylus* longus, stigmata exserta. *Capsula* perianthio brevior.

Allied to *J. rupestris* and sometimes confounded with that species, but distinguished by the broader green leaves, the umbellate inflorescence, aristate bracts and perianth, and the much longer anthers. *J. umbellatus* is a stouter plant than *J. rupestris*.

The type is Adamson 314 !

Damp sandy places in south-western Cape :—Oliphant's River, Clanwilliam, Adamson ! Malmesbury, *Schlechter* 1606 ! Berg River, Wellington, Adamson 313 ! 314 ! Fishhoek, *Levy* ! Unlocalised, *Zeyher* 46, p.pt. !

*Ranunculus Ficaria* Linn.: life-history and pollination.

By E. M. MARSDEN-JONES, F.L.S.

(With 10 Text-figures)

[Read 27 April 1933]

*RANUNCULUS FICARIA* is very widely distributed in Britain, occurring in all the vice-counties (1). It is to be found in two forms, one with bulbils in the axils of the leaves and one without. L. N. H. Larter (2), lately working at the John Innes Horticultural Institution, Merton, kindly examined samples of both forms and found that the somatic chromosome number in the non-bulbil-producing plants is  $2n=16$ , diploid, and in the bulbil-producing plants  $2n=32$ , tetraploid. Several plants of each form were examined. A. N. Wilcox, working at the same Institution, has been kind enough to examine further samples of bulbil-producing plants with the same result, so it may be assumed that bulbil-producing plants are tetraploid.

TABLE I.—Points of difference between non-bulbil- and bulbil-producing plants growing in the same locality.

Non-bulbil-producing plants.	Bulbil-producing plants.
No bulbils in axils of leaves.	Bulbils in axils of leaves.
Petals usually broad, overlapping, 8–13.	Petals usually narrow, not overlapping, 7–11.
Stamens 19–49.	Stamens 14–26.
Pollen viable, mixed with non-viable grains.	Pollen viable, with a larger proportion of non-viable grains.
Carpels 11–72.	Carpels 5–44.
Seeds judged to be viable, per head 0–39.	Seeds judged to be viable, per head 0–6.
Reproduction. Sexual.	Reproduction. Almost completely vegetative.
Somatic chromosomes $2n=16$ , diploid.	Somatic chromosomes $2n=32$ , tetraploid.

A distinction must be made between the two forms, as it will be seen from Table I they differ considerably in several points. The three fundamental ones by which the bulbiferous form differs is in the production of bulbils in the axils of the leaves, in reproduction being almost completely vegetative, and in the number of chromosomes. I propose, therefore, that the plants which produce bulbils be called *R. Ficaria* var. *bulbifera*.



*RANUNCULUS FICARIA* Linn. var. *BULBIFERA*, nov.

*Bulbulis* in foliorum caulinorum axillis evolutis; *perianthii* segmentis 7-11, plerumque angustis oblongisque, haud imbricatis; *staminibus* 14-26, polline minime fertili; *achenis* 5-44, seminibus fertilibus nullis rarissime (usque ad 6); reproductione plerumque asexuali; *chromosomatibus* somaticis tetraploideis ( $2n=32$ ).

My experience from observations made during the past ten years on individual plants is that they remain constant, either for bulbil or non-bulbil production. There is, so far as I know, no census for the distribution of var. *bulbifera*.

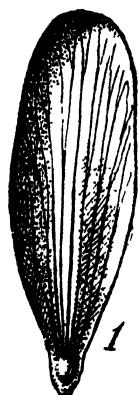
Non-bulbil-producing plants and var. *bulbifera* grow together in several places at Potterne, in shady spots, and in one place on a sunny hedge-bank. I have never seen var. *bulbifera* growing in full sun in meadows; it generally confines itself to shady places and damp hedge-banks. It does not follow, however, that these plants are always to be found in such localities; they are often absent and only non-bulbil-producing plants occur. The non-bulbil-producing plant is much more frequent than var. *bulbifera*, which is rather restricted in habitat.

*R. Ficaria* is usually hermaphrodite, but it may also be gyno-monoecious and trioecious. I have seen plants at Potterne and Kew which were definitely female and others which were both hermaphrodite and female, the hermaphrodite flowers generally with a reduced number of stamens. I have not yet seen a female plant which was constant for that character from year to year; neither have I found plants with male flowers only, except in Wiltshire. They are characterised by having petaloid sepals, 1.7 cm. long and 1.1 cm. broad, without nectaries, and the carpels abortive or completely absent. The number of stamens is greater than in hermaphrodite flowers, up to sixty-eight, producing viable pollen. Plants with double and semi-double flowers occur.

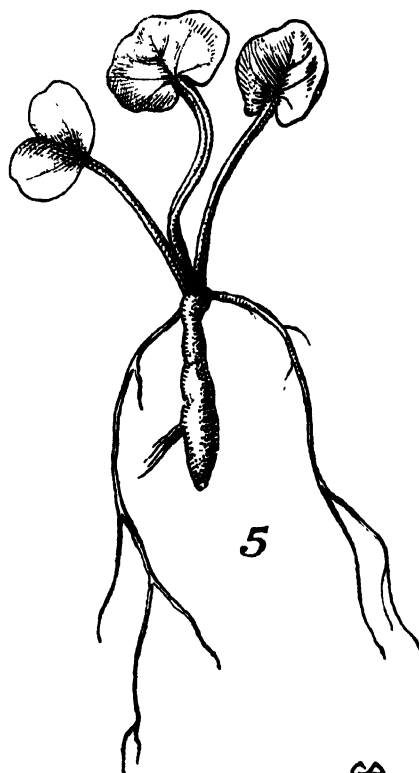
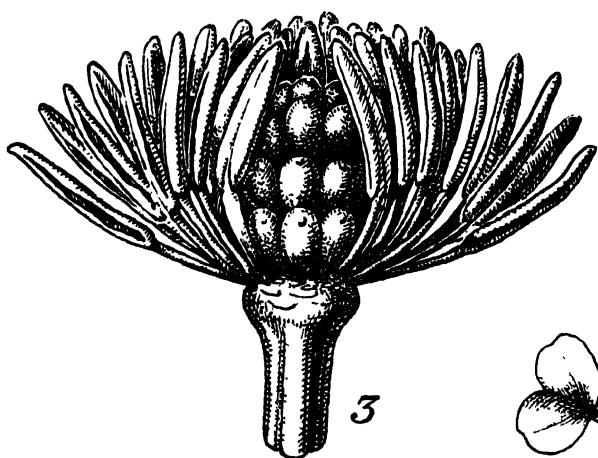
The colour of the flower is usually *lemon chrome*, although plants with *cadmium yellow*, *lemon yellow*, *barium yellow*, *naphthalene yellow*, and *white flowers* are to be found (3). The expanded corollas of individual plants vary, according to my observation, from 1.5 cm. to 4.5 cm. in diameter. The petals also vary from seven to thirteen, in length from 6 mm. to 2.5 cm., and in breadth from 3 mm. to 10 mm. These measurements are taken from the broadest petals. The sepals are usually three, but plants with four are not infrequent, in length from 5 mm. to 10 mm., and in breadth from 3 mm. to 6 mm.

Pollen and nectar are accessible to short-lipped insects, the nectar being secreted in a small scale at the base of the petal (fig. 1). The flowers are slightly

FIGS. 1-5. 1. Petal with nectary at base ( $\times 2$ ). 2 a. Front view of anther before dehiscence ( $\times 4$ ). 2 b. Back view of anther after dehiscence ( $\times 4$ ). 2 c. Side view of anther after dehiscence ( $\times 4$ ). 3. Position of stamens in relation to carpels ( $\times 4$ ). 4. Seedling just germinated ( $\times 2$ ). 5. Seedling ten weeks old (natural size).



2



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protandrous, and the anthers dehisce extrorsely (fig. 2, *a*, *b*, *c*). In the first stage the outer stamens bend towards the petals and their anthers dehisce before the stigmata are receptive. In the second stage the inner stamens arch over and stand above the carpels (fig. 3), and although the anthers dehisce extrorsely, failing insect visits self-pollination takes place, and if the plant is not self-sterile a small proportion of seed is set. The number of stamens varies very considerably, from fourteen to forty-nine, excluding those of the male plants. The average length of the outer stamens in hermaphrodite flowers is 6 mm., that of the inner stamens 8 mm.

It was easy to collect abundance of seed from non-bulbil-producing plants, but in var. *bulbifera* it was with extreme difficulty and only after a lengthy search that ten seeds which appeared to be viable were found. On 2 August 1930 a hundred seeds from non-bulbil-producing plants were sown in four pots, twenty-five seeds in each pot, and the ten seeds from var. *bulbifera* in another pot. The results of this experiment are given in Table II, and show the number of seeds which germinated and the approximate time of germination.

TABLE II.—*Germination test. Seed sown 2 August 1930.*

Pots 1–4, twenty-five seeds per pot from non-bulbil-producing plants.

Pot 5, ten seeds from var. *bulbifera*.

Pot 1, 25.	Pot 2, 25.	Pot 3, 25.	Pot 4, 25.	Pot 5, 10.	Germination.	
2	3	0	0	0	24 February 1931.	
2	2	2	1	0	Between 24 February and 15 March.	
13	13	13	15	0	Between 15 March and 12 April.	
1	0	2	1	0	Between 12 April and 26 April.	
0	0	1	0	0	Between 26 April and 25 May.	
18	18	18	17	0	Total germination of seed from non-bul- bil-producing plants, 71%.	Total germination of seed of var. <i>bulbi- fera</i> , 0%.
72%.	72%.	72%.	68%.	0%.	Average 71%.	Average 0%.

It will be seen from this Table that the maximum germination took place between 15 March and 12 April, the first seedlings appearing on 24 February, and the last (one only) between 26 April and 25 May.

The seeds of *R. Ficaria* always germinate in the early spring and germination is continuous. This fact is not deduced from this experiment only, but is supported by many other observations.

There is a most striking difference between the viability of seeds obtained from non-bulbil-producing plants and those of var. *bulbifera*. The former gave an average germination of 71 per cent., which may be considered satisfactory, while the latter gave no germination. If the seeds of var. *bulbifera* had been viable a comparable percentage with those of the non-bulbil-producing plants might reasonably have been expected, even allowing for the small number of seeds. It will be noticed that in pots 1 to 4 germination was most regular (figs. 4 & 5). This experiment clearly suggests that to judge viability from the appearance of the seed only may lead to erroneous conclusions. During the discussion following the reading of this paper Miss A. C. Halket (4) questioned the statement that var. *bulbifera* produces no seed capable of germination, and referred to tests she had herself made. So in 1933 I collected, after much search, fifty seeds of var. *bulbifera* which were sown on 4 August.

TABLE III.—*Germination test. Seed sown 4 August 1933.*

Pots 1-5, ten seeds per pot from var. *bulbifera*.

Pot 1, 10.	Pot 2, 10.	Pot 3, 10.	Pot 4, 10.	Pot 5, 10.	Germination.
1	..	..	..	..	10 January 1934.
1	..	..	..	..	16 January.
..	..	1	..	..	17 January. *
1	..	..	..	..	19 January.
..	..	1	..	..	24 January.
1	1	..	..	..	26 January.
1	..	..	..	..	28 January.
..	..	1	..	..	17 March.
5	1	3	0	0	Total germination, 18%.
50%.	10%.	30%.	0%.	0%.	Average 18%.

The result of this further test appears in Table III, from which it will be seen that a small proportion (18 per cent.) germinated. The number of seeds used in the previous test was evidently too small. My statement (5) that no viable seed is produced must therefore be modified.

In Table IV the results of an experiment made to test the viability of bulbils obtained from the axils of the leaves of var. *bulbifera* are given (fig. 6, bulbil in axil of leaf). On 12 June 1930 a hundred bulbils were planted in five pots, twenty bulbils in each pot.

It was surprising how quickly the plants produced from bulbils developed (figs. 7 & 8). On 26 April 1931 four plants had reached the flowering stage,

three flowered, and one formed a bud which did not open ; it is probable that most of the plants would have flowered the second year. No seedlings flower the first year, a proportion the second, and the remainder the third.

The growth of 81 per cent. of the bulbils is very interesting, as it gives some idea of the rate with which var. *bulbifera* increases. The plants produce

TABLE IV.—*Viability test of bulbils from the axils of the leaves of var. bulbifera, twenty bulbils per pot. Planted 12 June 1930.*

Pot 1, 20.	Pot 2, 20.	Pot 3, 20.	Pot 4, 20.	Pot 5, 20.	Growth.
6	6	6	2	4	25 November 1930.
3	1	2	5	8	Between 25 November and 17 December.
7	8	9	9	4	Between 17 December and 15 March, 1931.
0	0	1	0	0	15 April.
16	15	18	16	16	Total growth, 81%.
80%.	75%.	90%.	80%.	80%.	Average 81%.

axillary bulbils very prolifically, and counts were made to ascertain the number produced per plant by ten plants collected at random. The numbers are as follows :—(1) 31, (2) 6, (3) 44, (4) 17, (5) 30, (6) 12, (7) 53, (8) 26, (9) 7, (10) 15, giving a total of 241 for the ten plants. From Table IV the expectation is that at least 81 per cent. of these bulbils would be viable and that the progeny of the ten plants would be 195, most of which would probably flower the second year.

To obtain data for the number of viable and abortive seeds produced per head, and the total per plant, of plants growing in full sun, in shade, and by var. *bulbifera* ten of each were collected and counts made (figs. 9 & 10). In var. *bulbifera* any plants that produced seed which appeared to be viable were selected, but it must be stressed that very great difficulty was experienced in finding such plants.

FIGS. 6–10. 6. Bulbil in axil of leaf of var. *bulbifera* (natural size). 7. Bulbil just starting into growth ( $\times 2$ ). 8. Plant grown from bulbil twenty-four weeks old (natural size). 9. Fruiting head of a non-bulbil-producing plant showing viable and non-viable seeds ( $\times 4$ ). 10. Fruiting head of var. *bulbifera* showing a few swollen but non-viable seeds ( $\times 4$ ).



*Counts of apparently viable and abortive seeds produced by ten non-bulbil-producing plants growing in full sun. 26 May 1930.*

	Fruiting heads.	Viable.	Abortive.		Fruiting heads.	Viable.	Abortive.
(1)	1 . . . . .	28	0	(6)	1 . . . . .	26	4
	2 . . . . .	29	1		2 . . . . .	14	6
	3 . . . . .	25	4		3 . . . . .	22	3
	4 . . . . .	25	5		4 . . . . .	31	1
	5 . . . . .	27	3		5 . . . . .	14	11
		<hr/>	<hr/>			<hr/>	<hr/>
		134 (91%).	13 (9%).			107 (81%).	25 (19%).
		<hr/>	<hr/>			<hr/>	<hr/>
(2)	1 . . . . .	17	5	(7)	1 . . . . .	20	1
	2 . . . . .	18	5		2 . . . . .	21	6
		<hr/>	<hr/>		3 . . . . .	26	3
		35 (78%).	10 (22%).		4 . . . . .	21	7
		<hr/>	<hr/>			<hr/>	<hr/>
						88 (84%).	17 (16%).
(3)	1 . . . . .	23	4			<hr/>	<hr/>
	2 . . . . .	33	4	(8)	1 . . . . .	19	2
	3 . . . . .	25	5		2 . . . . .	13	5
	4 . . . . .	22	4		3 . . . . .	4	14
	5 . . . . .	19	15			<hr/>	<hr/>
	6 . . . . .	19	12			36 (63%).	21 (37%).
		<hr/>	<hr/>			<hr/>	<hr/>
		141 (76%).	44 (24%).				
		<hr/>	<hr/>				
(4)	1 . . . . .	13	13	(9)	1 . . . . .	11	7
	2 . . . . .	18	6		2 . . . . .	11	8
	3 . . . . .	18	8		3 . . . . .	14	2
		<hr/>	<hr/>			<hr/>	<hr/>
		49 (64%).	27 (36%).			36 (68%).	17 (32%).
		<hr/>	<hr/>			<hr/>	<hr/>
(5)	1 . . . . .	20	8	(10)	1 . . . . .	19	4
	2 . . . . .	31	1		2 . . . . .	21	2
	3 . . . . .	21	4		3 . . . . .	12	11
		<hr/>	<hr/>			<hr/>	<hr/>
		72 (85%).	13 (15%).			52 (75%).	17 (25%).
		<hr/>	<hr/>			<hr/>	<hr/>

TOTALS :—

Apparently viable.  
750 (79%),

Abortive.  
203 (21%).

*Counts of apparently viable and abortive seeds produced by ten non-bulbil-producing plants growing in shade. 26 May 1930.*

Fruiting heads.			Fruiting heads.		
	Viable.	Abortive.		Viable.	Abortive.
(1)	1 ..... 0	25	(7)	1 ..... 0	29
	2 ..... 17	11		2 ..... 25	14
	3 ..... 7	4		3 ..... 17	30
	4 ..... 17	8		4 ..... 15	21
	—	—		5 ..... 17	21
	<u>41 (46%).</u>	<u>48 (54%).</u>		6 ..... 4	26
(2)	1 ..... 4	21		—	—
	2 ..... 0	23		<u>78 (36%).</u>	<u>141 (64%).</u>
	3 ..... 0	20	(8)	1 ..... 12	14
	—	—		2 ..... 7	17
	<u>4 (6%).</u>	<u>64 (94%).</u>		3 ..... 8	18
(3)	1 ..... 9	15		4 ..... 20	5
	2 ..... 16	6		5 ..... 15	6
	3 ..... 9	20		6 ..... 13	7
	4 ..... 0	22		7 ..... 14	9
	5 ..... 0	28		8 ..... 2	23
	—	—		—	—
	<u>34 (27%).</u>	<u>91 (73%).</u>		<u>91 (48%).</u>	<u>99 (52%).</u>
(4)	1 ..... 19	15	(9)	1 ..... 9	5
	2 ..... 18	12		2 ..... 6	10
	3 ..... 25	6		3 ..... 4	9
	4 ..... 15	13		4 ..... 8	11
	—	—		—	—
	<u>77 (63%).</u>	<u>46 (37%).</u>		<u>27 (44%).</u>	<u>35 (56%).</u>
(5)	1 ..... 20	21	(10)	1 ..... 22	2
	2 ..... 0	39		2 ..... 15	15
	3 ..... 25	13		3 ..... 20	7
	4 ..... 24	9		4 ..... 24	7
	5 ..... 14	20		5 ..... 19	14
	6 ..... 30	2		—	—
	—	—		<u>100 (69%).</u>	<u>45 (31%).</u>
	<u>113 (52%).</u>	<u>104 (48%).</u>			
(6)	1 ..... 28	10			
	2 ..... 33	2			
	3 ..... 29	7			
	4 ..... 31	9			
	5 ..... 5	35			
	6 ..... 6	31			
	7 ..... 14	20			
	—	—			
	<u>146 (56%).</u>	<u>114 (44%).</u>			

TOTALS :—

Apparently viable.  
711 (47%).

Abortive.  
787 (53%).



*Counts of apparently viable and abortive seeds produced by ten plants  
of var. bulbifera. 26 May 1930.*

	Fruiting heads.	Viable.	Abortive.		Fruiting heads.	Viable.	Abortive.
(1)	1 . . . .	0	29	(6)	1 . . . .	0	17
	2 . . . .	0	31		2 . . . .	0	19
	3 . . . .	0	27		3 . . . .	0	12
	4 . . . .	0	30		4 . . . .	0	18
	5 . . . .	0	26		5 . . . .	0	15
	6 . . . .	0	20			—	—
	7 . . . .	0	17			0 (0%).	81 (100%).
		—	—			—	—
		0 (0%).	180 (100%).	(7)	1 . . . .	0	8
		—	—		2 . . . .	4	9
(2)	1 . . . .	0	18		3 . . . .	0	14
	2 . . . .	1	19		4 . . . .	0	16
	3 . . . .	1	18		5 . . . .	0	18
	4 . . . .	0	15		6 . . . .	0	16
	5 . . . .	2	8		7 . . . .	0	17
	6 . . . .	1	12		8 . . . .	0	10
	7 . . . .	1	14			—	—
		—	—			4 (4%).	108 (96%).
		6 (5%).	104 (95%).			—	—
		—	—	(8)	1 . . . .	0	34
(3)	1 . . . .	1	11		2 . . . .	0	13
	2 . . . .	4	16		3 . . . .	0	27
	3 . . . .	0	11		4 . . . .	0	20
	4 . . . .	0	17		5 . . . .	0	28
	5 . . . .	0	10			—	—
	6 . . . .	0	17			0 (0%).	122 (100%).
	7 . . . .	0	10			—	—
	8 . . . .	0	11			—	—
		—	—	(9)	1 . . . .	0	18
		5 (5%).	103 (95%).		2 . . . .	0	22
		—	—		3 . . . .	0	20
(4)	1 . . . .	0	16		4 . . . .	0	20
	2 . . . .	0	15			—	—
	3 . . . .	0	16			0 (0%).	80 (100%).
		—	—			—	—
		0 (0%).	47 (100%).	(10)	1 . . . .	0	30
		—	—		2 . . . .	0	28
(5)	1 . . . .	0	15		3 . . . .	0	17
	2 . . . .	2	13			—	—
	3 . . . .	3	11			0 (0%).	75 (100%).
	4 . . . .	2	7			—	—
	5 . . . .	1	13			—	—
		—	—			—	—
		8 (12%).	59 (88%).			—	—
		—	—			—	—

TOTALS :—

Apparently viable.  
23 (2%).

Abortive.  
959 (98%).

The figures for seed production of the sun and shade non-bulbil-producing plants are interesting, but they are open to modification. From the results obtained for the germination of seed from the non-bulbil-producing plants, it is possible that the percentage of viable seed given, i.e. seed that will germinate, is too high. There was no difficulty in obtaining a definite count of the abortive seeds, but for viability it was entirely a question of judgment; seeds that were hard and plump were presumed to be viable. Owing to their fugaceous nature, the seeds had to be counted before they were quite ripe, so it was not possible to prove their viability by a germination test. The seeds that were used in the germination test given in Table II, however, were collected from plants growing in or near the same localities as the plants collected for the counts. It may be assumed that if 29 per cent. be written off the totals a fair presentation of the number of seeds capable of germinating will be shown. The fact that 29 per cent. failed to germinate does not necessarily mean that they were not viable, for slugs or insects might possibly have browsed some off before the counts were made; indeed this once obviously happened, a small piece remaining to indicate the damage.

The ten sun plants had only thirty-seven fruiting heads as against fifty-two from those growing in shade; it was possible, however, to pick out five from each set which had the same number, and with only a small difference in the amount of viable and abortive seed produced.

TABLE V.—*Five non-bulbil-producing plants from sun and shade with the same number of fruiting heads, showing to what extent seed production varies.*

Sun plants.				Shade plants.			
Plant.	Fruiting heads.	Viable seeds.	Abortive seeds.	Plant.	Fruiting heads.	Viable seeds.	Abortive seeds.
3 .....	6	141	44	5 ....	6	113	104
1 .....	5	134	13	3 ....	5	34	91
6 .....	5	107	25	10 ....	5	100	45
7 .....	4	88	17	4 ....	4	77	46
9 .....	3	36	17	2 ....	3	4	64
Totals .	23	506 (81%).	116 (19%).	Totals .	23	328 (48%).	350 (52%).

From the totals given in Table V it will be seen that the viable seed produced by the sun plants is 62 per cent. more than the abortive, and by the shade plants 4 per cent. less. The viable seeds produced by the sun plants are 33 per cent. more than the shade plants. The difference of 33 per cent. is, from the point of view of the number of insects visiting the sun plants, not as great as might have been expected. The explanation of this difference

has been obtained from the pollination observations made on shade plants. The term "shade plants" is only relative, for until the trees are nearly in full leaf sun is not altogether excluded from such plants during some part of the day; quite a number of insects visit them, and in places where the sun penetrated three species of Hymenoptera were seen. Two species of *Meligethes* were very frequent. These beetles undoubtedly play a very important part in the pollination of *R. Ficaria*, especially shade plants where other insects are not so frequent. They crawl about the flowers, getting well dusted with pollen; indeed, they are often yellow with it. I never saw them move from flower to flower, probably because they are rather small. In order to determine this point I removed them from certain plants; these I examined a few hours later and found them again to contain beetles. This experiment was repeated with the same result, and strongly suggests that they not only move from flower to flower, but from plant to plant, and in so doing carry pollen and effect cross-pollination. Mr. K. G. Blair of the British Museum (Natural History) informs me that they fly readily.

Taking into consideration the fact that *R. Ficaria* flowers early, and that there are many days when the weather is not favourable for insect visits, coupled with great self-sterility, the percentage of apparently viable seeds produced by both sun and shade plants may be considered good.

The attempts to judge by sight the viability of seeds produced by var. *bulbifera* was very much complicated by the fact that early in the fruiting stage many plants appear to be seeding normally, but as bulbil-production increases so deterioration of the seeds sets in. This continues till practically nothing but shrivelled seeds remain, with an occasional one which looks as if it might be viable. It is possible that the 2 per cent. of apparently viable seed from the ten plants of var. *bulbifera* would have been reduced had the counts been made even a week later. The deterioration of a supposedly viable seed to a shrivelled one takes place very rapidly.

In 1933 a further count of seeds from fifty plants of var. *bulbifera* was made, the total number being 3138, of which 92 were apparently viable and 3046 abortive, 3 per cent. against 97 per cent. From the result of the germination test given in Table III only 18 per cent. of the above 3 per cent. might be expected to germinate. This count brings out most clearly the very small proportion of apparently viable seed produced by var. *bulbifera*. These fifty plants had 250 fruiting heads, of which only sixty (24 per cent.) produced any apparently viable seed.

Van Tieghem (6) makes the assertion that '... the fertilisation of the ovules in the bulbil-producing *Ficaria* is impossible because no pollen is ever formed in the stamens', a statement which is credited to Chatin by Darwin (7) and Knuth (8). In Britain, according to my own observations, var. *bulbifera* produces pollen, a proportion of which is viable. Even supposing this were not so, the production of seed would not be prevented, for insects would carry pollen from non-bulbil-producing plants. Van Tieghem pollinated flowers

of var. *bulbifera* with pollen from the non-bulbil-producing form but obtained no seed ; he nevertheless observed plants of var. *bulbifera* which had produced a few ripe seeds. There is no suggestion that he sowed any of these seeds. In 1932 the experiment of removing the bulbils from the axils of the leaves of var. *bulbifera* was carried out. Twelve plants were selected for observation, six were allowed to produce bulbils normally, the other six had their bulbils removed as soon as they formed ; the plants were examined every second or third day. None of these plants produced a single viable seed, deterioration was as complete in the de-bulbilled plants as in those that were not so treated. When this experiment was carried out I had not seen Kindler's (9) paper ; she pollinated twenty plants of var. *bulbifera* after removing the bulbils. Her results were similar to mine, with the exception that some of her plants produced a few ripe seeds.

The probable reason why little or no viable seed is produced by de-bulbilled plants is that the bulbils have to be formed before they can be removed ; they form with great rapidity. Formation starts about the beginning of April and reaches its maximum in May. The fact that before bulbil-production is at its maximum seeds appear to be developing normally, and when the maximum of bulbil-production is reached deterioration sets in, points to the conclusion that the nutriment required for the formation of endosperm is almost completely diverted to the production of bulbils. Under natural conditions var. *bulbifera* produces only a very small proportion of viable seed, many plants none. Sir Arthur W. Hill (10) carried out the experiment of cutting off the flower stalks of var. *bulbifera* near the ground-level and placing them in water and then removing the bulbils as they appeared. He was successful in obtaining viable seed. In 1933 I placed fruiting heads in water, after removing the bulbils, and also obtained viable seed. The result of these experiments lends additional support to my suggestion.

In considering pollination the question arises as to what extent seed production would be affected if insects failed to visit. *R. Ficaria* has its anthers so arranged that failing insect visits self-pollination takes place. The following experiment to determine this point was carried out : five plants were covered with tiffany cages after all the flowers that were open had been removed—the results are given in Table VI (p. 52).

From the figures given in Table VI it will be seen that when insects are excluded there is a very great falling off in the production of apparently viable seed. This is very marked when the large number of fruiting heads produced by most of these plants is taken into consideration. One plant was sterile ; this is no exception, as many plants on selfing have proved to be sterile, others have given results comparable with those obtained from plants 1 to 4. The conclusions drawn from this experiment are : (1) that plants of *R. Ficaria* are either completely self-sterile or produce only a small proportion of viable seed when self-pollination takes place, (2) that cross-pollination by insects is absolutely necessary for the maximum production of viable seed.

A series of pollination observations were made in order to determine the frequency of insect visits, the species which visit, and the object of their visits, whether in search of pollen, nectar, or both. Thirty-five observations were made between 15 March and 29 May 1931 under different weather conditions and

TABLE VI.—*Five non-bulbil-producing plants protected under cages to exclude insects for seed-production test.*

Number of fruiting heads.	Plant 1, 41.		Plant 2, 27.		Plant 3, 55.		Plant 4, 17.		Plant 5, 9.	
	Heads.	Seeds.	Heads.	Seeds.	Heads.	Seeds.	Heads.	Seeds.	Heads.	Seeds.
Seeds per head judged to be viable.	11	0	24	0	35	0	10	0	9	0
	2	1	2	1	4	1	4	1	..	..
	6	2	1	2	2	2	3	2	..	..
	4	3	..	..	8	3	1	3	..	..
	4	4	..	..	2	4	1	11	..	..
	3	5	..	..	1	6	..	..	..	..
	4	6	..	..	1	7	..	..	..	..
	2	7	..	..	1	9	..	..	..	..
	2	8	..	..	1	18	..	..	..	..
	2	13	..	..	..	..	..	..	..	..
	1	9	..	..	..	..	..	..	..	..
	1	10	..	..	..	..	..	..	..	..
Seeds judged to be viable per plant.	156		4		80		24		0	
Germination ex- pected from test made when an aver- age of 71% was obtained.	111		3		57		17		0	

in various localities. Twenty-six hours fifteen minutes were spent observing. Greenwich time is given for all the observations.

On 22 April maximum florifery was reached, on the 30th the flowers were slightly past their best and by 9 May there was a very considerable falling off in the number produced. On 15 May those in the open were nearly over, and on the 29th, when the last observation was made, only a small number of shade plants were in flower. On twenty-two occasions *Apis mellifica* was

observed visiting ; beetles of the genus *Meligethes* were seen on twenty-seven observations. Plants with pale flowers were observed to see how *Apis mellifica* would react to them—they were visited with as much regularity as the full yellow ones, no preference being shown for the latter.

The amount of sun per day is an important factor in pollination by insects, especially when spring flowers are concerned, as there is a considerable and rather sudden drop in temperature at this time of year when the sun becomes obscured. It was noticed that there was a great falling off in the number of insects visiting during the time the sun was not shining. In cold dull or wet weather insects were not seen to visit.

*Complete list of insects seen visiting R. Ficaria, their approximate frequency, and the object of their visits.*

COLEOPTERA : *Tachyporus hypnorum* F., ♂ and ♀, very frequent, pollen and nectar. *Meligethes rupipes* Gyll., ♂, once, nectar. *M. aeneus* F., ♂ and ♀, very frequent, pollen and nectar. *M. viridescens* F., ♂ and ♀, very frequent, pollen and nectar. *M. ovatus* Sturm, ♀ twice, pollen and nectar. *M. picipes* Sturm, ♂ and ♀, very frequent, pollen and nectar. *M. erythropus* Gyll., ♂ and ♀, very frequent, pollen and nectar. *Agriotes pallidulus* Ill., ♂ and ♀, frequent, pollen and nectar, but mostly nectar. *Bruchus atomarius* L., ♀, once, nectar.

HYMENOPTERA : *Halictus rubicundus* Christ., ♀, four times, pollen and nectar. *H. nitidiusculus* Kirb., ♀, once, nectar. *H. decipiens* Perk., ♀, four times, nectar. *H. morio* F., ♂ and ♀, four times, nectar. *Andrena albicans* Kirb., ♂, once, nectar. *A. trimmerana* Kirb., ♂ and ♀, three times nectar. *A. nitida* Fourc., ♂ and ♀, frequent, pollen and nectar. *A. gwynana* Kirb., ♂ and ♀, frequent, pollen and nectar. *A. chrysosceles* Kirb., ♀, once, nectar. *Nomada alternata* Kirb., ♂ and ♀, five times, nectar. *Bombus lapidarius* L., ♀, once, nectar. *B. terrestris* L., ♀, three times, nectar. *Apis mellifica* L., ♀, very frequent, pollen and nectar.

LEPIDOPTERA : *Vanessa urticae* L., ♀, four times, nectar. *Lycaena argiolus* L., ♀, once, nectar. *Micropteryx calthella* L., ♂ and ♀, frequent, nectar.

DIPTERA : *Rhamphomyia sulcata* Mg., ♀, twice, pollen and nectar. *Empis trigramma* Mg., ♂ and ♀, six times, nectar. *Chilosia albitalis* Mg., ♂ and ♀, frequent, pollen. *Platychirus albimanus* F., ♂ and ♀, frequent, pollen. *Melano-stoma mellinum* L., ♂ and ♀, very frequent, pollen and nectar. *Asca podagrica* F., ♀, twice, pollen. *A. floralis* Mg., ♀, three times, pollen. *Rhingia campestris* Mg., ♂ and ♀, six times, pollen and nectar. *Eristalis tenax* L., ♂ and ♀, frequent, pollen and nectar. *E. pertinax* Scop., ♂ and ♀, frequent, pollen and nectar. *E. nemorum* L., ♂ and ♀, three times, pollen and nectar. *Pollenia rudis* F., ♂ and ♀, four times, pollen and nectar. *Melinda caerulea* Mg., ♂, once, pollen and nectar. *Orthellia caesarion* Mg., ♂ and ♀, three times, pollen and nectar. *Pyrellia eriophthalma* Moq., ♂ and ♀, frequent, pollen and

nectar. *Musca autumnalis* Deg., ♂ and ♀, frequent, pollen and nectar. *Phaonia serva* Mg., ♂, once, pollen and nectar. *Coelomyia mollissima* Hal., ♂ and ♀, very frequent, pollen and nectar. *Pegohylemyia fugax* Mg., ♂, once, pollen and nectar. *P. discreta* Mg., ♀, once, nectar. *Egle aestiva* Mg., ♂ and ♀, frequent, pollen and nectar. *Scatophaga stercoraria* L., ♂ and ♀, very frequent, pollen and nectar. *Mosillus subsultans* F., ♂ and ♀, frequent, pollen and nectar.

*List of insects seen visiting plants growing in shade.*

COLEOPTERA : *Tachyporus hypnorum* F., ♂ and ♀, frequent, pollen and nectar. *Meligethes aeneus* F., ♂ and ♀, frequent, pollen and nectar. *M. picipes* Sturm, ♂ and ♀, very frequent, pollen and nectar. *Agriotes pallidulus* Ill., ♀, once, nectar.

HYMENOPTERA : *Andrena trimmerana* Kirb., ♀, once, nectar, *A. nitida* Fourc., ♂ and ♀, frequent, pollen and nectar. *Apis mellifica* L., ♀, frequent, pollen and nectar.

DIPTERA : *Rhamphomyia sulcata* Mg., ♀, twice, pollen and nectar. *Empis trigramma* Mg., ♂ and ♀, five times, nectar. *Melanostoma mellinum* L., ♂ and ♀, four times, pollen. *Eristalis pertinax* Scop., ♂, once, pollen and nectar. *Pyrellia eriophthalma* Mcq., ♂, four times, pollen and nectar. *Phaonia serva* Mg., ♂, once, pollen and nectar. *Coelomyia mollissima* Hal., ♂ and ♀, very frequent, pollen and nectar. *Pegohylemyia fugax* Mg., ♂, once, pollen and nectar. *P. discreta* Mg., ♀, once, nectar. *Egle aestiva* Mg., ♂ and ♀, five times, pollen and nectar. *Scatophaga stercoraria* L., ♂ and ♀, frequent, pollen and nectar.

#### SUMMARY.

1. *R. Ficaria* is very widely distributed in Britain, occurring in all the vice-counties. It is found in two forms, one producing bulbils in the axils of the leaves, the other not. The distribution of the former is not yet known.

2. The two forms differ also in that reproduction is almost completely vegetative in the bulbiferous form—its chromosomes ( $2n=32$ ) are twice as many.

3. The plants are usually hermaphrodite, but plants with hermaphrodite and female, male, or female flowers occur. The flower colour is usually *lemon chrome*. Pollen and nectar are accessible to short-lipped insects. Failing cross-pollination self-pollination takes place, but owing to great self-sterility only a small amount of viable seed results.

4. An average of 71 per cent. of seed from the non-bulbil-producing plants germinated ; there was no germination of any of the ten seeds from var. *bulbifera* in 1931. In 1933 a further fifty seeds of var. *bulbifera* were sown and an average germination of 18 per cent. was obtained. Seedlings do not flower until the second year, then only a small proportion.

5. A test to determine the viability of the bulbils produced in the axils of the leaves by var. *bulbifera* gave 81 per cent. growth; three of the plants flowered the first year.

6. Seed counts showed that sun plants produced 33 per cent. more viable seeds than the shade plants. This difference is accounted for by the fact that insects visit shade plants fairly frequently, and that beetles of the species *Meligethes* undoubtedly play an important part in pollination.

7. Weather conditions determine to a large extent the amount of viable seed produced. In wet cold weather the flowers remain closed and no insects visit. As some plants are partly, others completely self-sterile, insect visitors are absolutely necessary for the maximum output of viable seed.

8. In ten plants of var. *bulbifera* the seed judged to be viable was 2 per cent. In 1933 fifty plants had 3 per cent. seed judged to be viable and of this the germination expected would be 18 per cent.

9. Bulbils were removed from the axils of the leaves of var *bulbifera*, but even so no viable seed was produced. Under natural conditions var. *bulbifera* produces only a very small proportion of viable seed, many plants producing none.

10. Thirty-five observations were made, lasting for twenty-six hours and fifteen minutes between 15 March and 29 May 1931 to determine what insects visit *R. Ficaria*. A list of forty-eight species was obtained, comprising Coleoptera, Hymenoptera, Lepidoptera, and Diptera; many of these were frequent, but some were only seen once. *R. Ficaria* is adequately visited under suitable weather conditions.

I desire to thank Mr. K. G. Blair of the British Museum (Natural History) and Mr. J. E. Collin of Newmarket for kindly naming the insects, and Mr. G. Atkinson, artist to the Royal Botanic Gardens, Kew, for the excellent figures. I also wish to acknowledge the help I have received from my wife.

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## A contribution to the moss flora of Borneo.

By H. N. DIXON, M.A., F.L.S.

(PLATES 1-4)

[Read 22 November 1934]

FOR a country of such botanical richness and interest, the mosses of Borneo have received but slight attention. In Dr. Stapf's monumental work on the Flora of Kinabalu, only thirty-one species of mosses, seven new, are listed. Miss Gibbs's paper in Journ. Linn. Soc., 1914, contains eight records, one new. A certain number of older records are scattered over earlier works, such as Lacoste's (1), the 'Bryologia javanica', etc. Hampe's account of Beccari's collections gives fifty-three species, sixteen being new. In 1916 I published an account of Mr. Binstead's mosses, including fifteen new species. An important paper by Brotherus, published in 1928, based principally on the collections made by Hans Winkler in West Borneo, included thirty-eight new species, some half-dozen of which, unfortunately, must be reduced.

The above papers I believe practically exhaust the bryological literature of importance for the island. A bibliographical list is given below.

The present paper is based mainly on two important collections recently made. In Nov.-Dec. 1931, R. E. Holttum ascended Kinabalu, and made systematic collections of mosses, which further illustrate the richness and the remarkable interest of the flora of that mountain. The collection included one new genus, *Stephanodictyon*, and over twenty new species. Mr. Holttum has written for me a topographical note on his visit.

In the autumn of 1932 the Oxford University Expedition to Sarawak spent several months in the region of G. Dulit, and this too resulted in a large and valuable addition to our knowledge of the bryological flora of the island. P. W. Richards, by whom the mosses were collected, has written an account of the ecological conditions under which the mosses were noted. This collection also contained the type of a new genus, *Taxitheliella*, together with over thirty new species.

In addition to these collections, I have included several smaller ones. The principal one is a considerable number of unnamed specimens received from Mitten's herbarium in the New York Botanical Garden, collected by A. H. Everett. A rather large proportion of these were undescribed species.

I have also received from the Buitenzorg Botanical Garden for determination a number of mosses from Borneo by various collectors, e.g. Hallier, Endert, Hubert Winkler, &c.; while the Singapore Botanical Gardens have contributed a small number collected by C. Boden Kloss, C. M. Enriquez, H. N. Ridley, and others.

It will be seen that the list here given is the most important single contribution to the moss flora of Borneo that has appeared. Roughly, it includes records of some 300 species, of which 75 (including two new genera) are new to science, while 85 others are newly recorded from the island.

The considerable proportion of new forms and new records in all the collections indicates, however, that we are very far yet from having reached anything like an approach to a complete knowledge of the rich moss flora of this remarkable phyto-geographical area.

TOPOGRAPHICAL NOTE. By R. E. HOLTUM.

There have been many visitors to Kinabalu, and many accounts of the topography of the mountain. The most recent account is that by Messrs. H. M. Pendlebury and F. N. Chasen (*Journ. F.M.S. Museums*, vol. xvii, pp. 1-38, 1932), who visited Kinabalu in 1930 and covered much the same ground as myself. The most recent general account of the vegetation of the mountain is that of Miss Gibbs (*Journ. Linn. Soc., Bot.* xlii, 1914), who makes some reference to bryophytes, but evidently had no time to devote to collecting them. Miss Gibbs gives full reference to previous literature.

The moss collections here described were made between 5 and 27 November 1931. I was chiefly interested in ferns, and having no critical knowledge of mosses collected them rather casually and without detailed field-notes. The following paragraphs give some account of the nature of the country traversed, the prevalence of mosses, and the kind of situations in which I found them.

The approach to the mountain lies along the valley of the Kadamaian River. The lower part is almost entirely through cultivated areas, only the bottoms of the steepest side-valleys containing forest of any size. I collected a little in one such valley near Kabayau (600 ft.). Beyond Koung, which lies in the valley bottom at 1,300 ft., the path ascends to the right, gradually climbing to the top of the valley-side at Dallas (3,200 ft.), again through clearings and secondary growth. I descended into two small valleys below Dallas and collected near the streams. Beyond Dallas the path skirts the Dallas-Tenompok ridge, climbing gradually in nine miles to Tenompok (4,700 ft.). On the right-hand side of this part of the path there is primitive forest almost all the way, and towards Tenompok on the left (lower) side also. A number of small steep rocky valleys intersect the ridge, and contain interesting hygrophilous plants, but mosses were not specially abundant.

At Tenompok is a very rich high forest containing many small streams. The smaller vegetation is festooned with slender pendulous mosses and hepatics, and tree-trunks are thinly moss-covered, but the cushion type of moss is almost absent.

Climbing above Tenompok, one leaves the bridle-path and ascends the forest track up the crest of the main spur of the mountain. The spur is hummocky, parts narrow and steep, parts broadly sloping; the former carry small

trees, often much stunted, the latter good high forest. The small trees of the steeper more exposed places carry moss cushions, and on the ground are cushions of mosses and hepatics, the latter especially predominating at the higher altitudes. Beyond about 6,000 ft. altitude and up to about 9,000 ft. masses of *Mastigophora* and other hepatics of similar habit are the chief ground-cover in the open ridge forest, while in more sheltered places other hepatics occur. Mosses are also present, but are nowhere abundant in the ridge forest. Cushions of *Sphagnum* occur occasionally, but much less abundantly than on some mountains of the Malay Peninsula.

At Kamborangah, 7,200 ft. altitude, I descended obliquely into the upper Kadamaian valley, reaching the stream at a slightly lower altitude. As one descends below the ridge-top, one enters a zone with fine bamboo undergrowth ; in this the lower parts of trees and fallen logs are covered with hepatics, and sometimes on the bigger trees are large cushions of hepatics at intervals up the trunk. Somewhat lower there are a fair number of Dicranaceous moss-cushions on the ground and on fallen logs, but always hepatics are more abundant than mosses. As one approaches the stream, pendulous species of both mosses and liverworts appear on the low tree branches, finally in enormous abundance. I have never at any other place seen a growth of this kind to compare with that below Kamborangah. With the long pendulous bryophytes, of the most delicate kinds, were many pendulous ferns, including some of the biggest specimens of *Polypodium*, section Grammitis, I have seen. The air must be continuously saturated with moisture, from the spray of the cataracts of the stream as it rushes down its rocky bed. On the stem of a tall tree-fern I found large plants of *Spiridens Reinwardtii*.

The ridge forest at higher altitudes, from about 9,000 ft. to the limit of tree growth, is rather open and consists chiefly of *Leptospermum* and conifers. The bryophyte vegetation here is rather scanty, and species growing on the trees are particularly few (chiefly *Macromitrium*), but as soon as one descends from the ridge-top towards the stream, a little below Pakka (10,000 ft.), moister conditions again prevail. All the trees by the stream are loaded with bryophytes, more liverworts than mosses. On the rocks in the stream-bed were mosses, one of which was evidently often submerged, and clung so tightly that it was difficult to remove.

The vegetation of the open rocky summit region is well described by Miss Gibbs. Plants are confined to the narrow crevices which intersect the rock-surface and serve as drainage-channels. In these crevices, and occasionally spreading a little over the rock surface, are a considerable quantity of mosses, chiefly such as form close firm crusts or cushions. Where slabs of rock overhang a little above small watercourses, more sheltered conditions prevail ; ferns are entirely confined to such positions (Miss Gibbs does not mention them), and with them are mosses.

After descending by way of Kamborangah and Lobang to Kiau (the route followed by Miss Gibbs for both ascent and descent), I visited the Marei Parei

spur, and there collected a number of plants not previously found. I climbed the spur above the camp to about 7,000 ft., but found no *Sphagnum*. On the wet hillside below the camp, under a thin tree-growth of *Dacrydium* and *Leptospermum*, were some terrestrial mosses, *Macromitrium ochraceum* being particularly abundant. In the more shady forest at a slightly lower altitude (probably a little below 5,000 ft.) was *Sphagnum sericeum*, a thin growth beside the path. I have found this species growing under very similar conditions in the Peninsula, on Gunong Tahan. All other species of *Sphagnum* which I have noticed in the Malayan region grow in rather exposed places.

I never saw on Kinabalu such excessively mossy ridge forest as occurs close to the tops of some mountain in the Malay Peninsula; that is, stunted trees covered with a close growth composed almost entirely of mosses, hepatics being in a minority. I think the reasons are probably connected with continuity of clouding rather than with any edaphic peculiarities. The relative paucity of *Sphagnum* on Kinabalu may also be connected with questions of moisture.

ECOLOGICAL NOTES ON THE MOSSES COLLECTED BY THE OXFORD EXPEDITION  
TO SARAWAK. By P. W. RICHARDS.

The Base Camp of the Oxford Expedition was situated about 98 Km. from the coast of Sarawak at Long Ladjok (or Leju) (Lat.  $3^{\circ} 19' N.$ , Long.  $114^{\circ} 17' E.$ ) on the Tinjar River, a tributary of the Baram, and near the native village of Long Kapah. At this point the Tinjar is enclosed in a narrow valley between the great escarpment of Mt. Dulit on the south, averaging 1,200–1,400 m. high, and a range of hills on the north of which the highest point is Mt. Laiun (c. 1,200 m.). It was near the Base Camp and on the neighbouring mountains that the greater part of the collection was made, and it is to this region alone that the following notes refer.

At the lower altitudes there is a typical equatorial climate with a mean temperature of about  $27^{\circ} C.$ , varying little throughout the year, and a rainfall probably not much short of 250 cm.; there is no definite dry season.

The rocks of the district are sandstone and shales of Miocene age, deficient in lime, and weathering to form white sand or red clay and loam soils.

The natural vegetation of the whole region is evergreen rain-forest. There are small rice-fields near the native villages.

The following types of forest were recognized :—

- A. *Tropical rain-forest* (on all uncultivated land below about 970–1,100 m.).
- |   |  |   |
|---|--|---|
| { | Primary (virgin).                        | { <i>Mixed forest</i> (on clay and loam). |
|   | Secondary (on land formerly cultivated). | { <i>Heath forest</i> (on white sand).    |
- B. *Montane rain-forest* ('Moss Forest'). On Mts. Dulit and Laiun, above 970–1,100 m.

*Tropical rain-forest.***Mixed forest.**

Though the conditions of moisture and temperature seem favourable for mosses, the mixed lowland forest is much poorer in them than would be expected, and fewer species can be collected in a given area than in a European forest.

The bryophytic vegetation is almost entirely epiphytic, and no mosses grow on the ground except rarely on steep hill ridges. In such places *Fissidens crassinervis* was found several times, and *Microdus macromorphus* once. The absence of ground mosses is probably chiefly due to the continual rain of dead leaves, which tends to smother small and delicate plants, but the fact that mosses are found on the floor of the heath forest shows that other factors must also be involved.

Several different communities of epiphytic bryophytes can be distinguished in the mixed forest :—

(i) *High epiphytes* on the crowns of the taller trees (over 15 m. above the ground). These are more or less exposed to the sun, and between showers of rain may have to suffer considerable drought. They have a xeromorphic structure, and tend to be yellowish or whitish, not bright green. Though a number of hepatics belong to this community, there are very few mosses, the only common one being *Syrrhopodon Wallisii*.

(ii) *Shade epiphytes on the lower part of the trunk of the larger trees*. Many of the larger tree trunks are quite bare of mosses and they are seldom thickly covered. A fair number of species was noted, mostly Acrocarpi, especially *Syrrhopodon* and *Calymperes* spp.

(iii) *Shade epiphytes on the undergrowth trees* (and lianes). The branches of the small trees belonging to the lowest stratum (about 8 m. high) are often thickly overgrown with bryophytes, especially in stream valleys and other moist places. There is a rich flora of Musci, and many large and beautiful species are common, e.g., *Endotrichella elegans* and *E. sarawakensis*. A variety of growth-forms is represented, including a few pendent species. The mosses of this community are mostly bright green, often shining, and the leaves usually have large cells.

(iv) *Epiphyllae*. Leaves in the undergrowth are often thickly covered with bryophytes, especially in stream valleys. Epiphyllae also occur in the middle levels of the forest, but are absent in the canopy. Hepaticae are dominant in the epiphyllous community, but the following mosses are found: *Chaetomitrium setosum*, *C. ciliatum*, *Taxithelium convolutum*\*, *T. Gottscheanum*, *T. Werneri*, *Dimorphocladon borneense*\*. The two species marked with an asterisk are confined to this habitat, the others also occur in (iii).

Other moss communities of the mixed forest are :—

(v) *Community on rotten logs*. Fallen logs are nearly always thickly covered with bryophytes. This is the only bryophytic community in the lowland

rain-forest, in which Musci are more abundant than Hepaticae. Except for the common *Leucobryum sanctum* Pleurocarpi predominate (Hypnaceae and Sematophyllaceae especially).

(vi) *Community on rocks and stones.* Rocks in the mixed forest were always fairly thickly covered with mosses and hepatics as far as the growth of ferns and small herbs allowed. On small loose lumps of sandstone *Pseudorhacelopus borneensis* was very characteristic: the protonema formed a complete covering over the surface, the leafy shoots being scattered at wide intervals.

On the mountains above 450 m. the mixed forest becomes damper, and, owing to the unevenness of the ground, the canopy becomes less continuous and allows more light to reach the undergrowth. Mosses become more abundant and a considerable number of species not found at lower altitudes appear, e.g. *Ephemeropsis tjibodensis* (epiphyllous), *Syrrhopodon Richardsii*, *Rhacopilum spectabile*. Ground mosses are rather more frequent than on the low ground, and may even occur where the slope is not very steep, e.g. *Leucobryum javense*.

#### Heath Forest.

This forest, which corresponds to the Heidewald of south-east Borneo (*H. Winkler*, Engler's Bot. Jahrb. l. 1914, p. 202), is a peculiar type of evergreen tropical rain-forest found only on white sand soils. It was met with on the southern slopes of Mt. Dulit at 800–1,100 m. (Koyan Valley) and also outside the Dulit area in the Marudi Forest Reserve on the Baram at a few feet above sea-level. It differs from the mixed forest in the better illuminated and denser undergrowth and has a very characteristic flora of flowering plants.

The moss flora also is very distinctive and different from that of the mixed forest. Mosses are more abundant, especially in the undergrowth, and probably if equivalent areas were compared the number of species would be greater.

Among the commoner heath forest mosses which are absent or rare in the mixed forest are *Cladopodanthus truncatus*, several species of *Syrrhopodon*, *Rhaphidostichum ramulinum*, and *Acroporium laevibogoricum*.

Several of the species common in the heath forest in the Koyan Valley (at 800 m.) and at Marudi (at near sea-level) were found in the mixed forest only above about 450 m., e.g. *Leucobryum javense*, *Mniomalia semilimbata*, *Rhizogonium longiflorum*, *Trismegistia lancifolia*.

Some species which were very common in the mixed forest were rare in the heath forest, e.g. *Endotrichella sarawakensis*.

A very striking difference from the mixed forest is the frequency of mosses on the ground: many of them were robust Leucobryaceae (*Schistomitrium Copelandii*, *Cladopodanthus truncatus*, *Leucobryum scalare*, *L. javense*, *L. aduncum*, *L. sanctum*, *Leucophanes candidum*, *Syrrhopodon scalariformis*, *S. Gardneri*, and *S. patens*, *Acanthorrhynchium subintegrum*).

Communities of epiphytic bryophytes can be distinguished corresponding to those of the mixed forest, but the composition of each is different. Hygro-morphic mosses such as the Hookeriaceae are scarcer than in the mixed forest, and the whole moss-flora has a more xerophilous appearance.

No doubt the better illumination\* and the probably rather lower humidity of the undergrowth are largely responsible for the characteristic moss-flora of the heath forest, but other factors must also play some part.

#### Secondary forest.

The moss flora of the older secondary forests does not differ much from that of the primary forests on the same kind of soil, but is always poorer.

#### *Lowland rivers and streams.*

No aquatic mosses were found either on stones or wood in the Tinjar, perhaps because of its muddiness and the sudden fluctuations of level to which it is liable. On mud-banks laid bare when the river level was low in July and August a few small mosses sprang up (*Microdus Miquelianus*, *Fissidens longevaginatus*, *F. sylvaticus*, and *Barbula obscuriretis*, also one hepatic). This community may be compared with that of *Physcomitrella*, &c., in similar habitats in Europe. *Calymperes Beccarii* is a characteristic species of tree-roots on the river bank.

Rocks and wood in and by the smaller forest streams and the torrents descending from the mountains have a rich moss flora including some large and handsome species such as *Hypopterygium ceylanicum* and *Mniodendron Korthalsii*, also many Hookeriaceae: most of the species do not occur in the forest away from the streams.

#### *Montane rain-forest ('mossy forest').*

All the upper part of Mt. Dulit above a height varying from about 970 to 1,100 m. and the extreme summit of Mt. Laiun (c. 1,200 m.) are covered with a dwarf forest entirely different in character from the lowland forest, and often called, from its most striking feature, mossy forest. Forest of this type was also met with on Mts. Mulu and Santubong, and seems to be found on most of the higher mountains in the Malayan region. At 1,230 m. on Dulit the mean temperature was about 5°·5 C. (10° F.) lower than at the Base Camp in the Tinjar Valley (alt. about 100 m.). Rainfall was more frequent, and the total amount no doubt greater than at low altitudes. Mist and cloud were very frequent, and the relative humidity of the air was normally very high. Dry spells lasting for several days do, however, occur, and at such times the epiphytic mosses are liable to dry up to some extent.

The trees of the mossy forest are under 18 m. high and cast a less deep shade than that of the lowland forests. There are extremely few species of flowering plants common to the mossy forest and the lowland rain-forest, and the boundary between the two types of vegetation is remarkably sharp.

In the bryophytic vegetation of the mossy forest, as in that of the lowland forest<sup>†</sup>, Hepaticae are much more abundant than Musci. The enormous conical

\* The distribution of *Leucophanes candidum*, which is common on and near the ground in the heath forest at Marudi, but at Dulit is found only in the tops of tall trees in the mixed forest, is presumably determined chiefly by the difference in illumination.



masses of epiphytic bryophytes which conceal the lower part of the tree-trunks, formed mainly by *Mastigophora diclados*, species of *Bazzania*, *Lepidozia*, *Schistochila*, &c. Though true mosses play only a subordinate rôle, they are represented by a large number of species, many of which are large and conspicuous. As with the flowering plants there are very few species found in both the mossy forest and the lowland forest, and the two moss floras are separated by a sharp boundary. This is illustrated by the following figures :—

Number of species in the tropical rain-forest (mixed and heath).	Number of species in the montane rain-forest.	Number of species in common.
119	53	12

Or if the species found only in or near streams (which tend to be widely distributed) are omitted, the figures are :—

94	48	8
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Several whole genera are highly characteristic of the mossy forest or the lowland forest respectively. Thus *Fissidens* is represented by ten species in the lowlands, but is quite absent in the mossy forest; *Syrrhopodon* by thirteen species in the lowlands and only three in the mossy forest; *Endotrichella* and all the genera of Hookeriaceae are mainly lowland. On the other hand, *Sphagnum*, *Dicranoloma*, and the Hypnodendraceae are almost confined to the mossy forest and *Acroporium* is much more richly represented there than elsewhere.

In the mossy forest bryophytes occur in enormous abundance on shrubs and on the lower part of the tree-trunks up to a height varying from about 2 to 3 m. in the more open places to at least 10 m. in the shadier parts: above this height the luxuriant growth suddenly stops, bryophytes are relatively scarce and tend to grow in compact tufts. Two main epiphytic communities may therefore be distinguished :—

(i) *High epiphytes* growing above this line. Only three species of mosses were found in this community, viz. *Macromitrium ochraceum*, *Cladopodanthus speciosus*, and *Syrrhopodon borneensis* var. *robustus*. Others no doubt occurred, but were difficult to collect for obvious reasons.

(ii) *Low epiphytes* growing at lower levels. These include numerous species of *Acroporium*, *Dicranoloma*, &c., and a very large number of hepatics.

Other communities of bryophytes in the mossy forest are :—

(iii) *Epiphyllae*. These are less abundant than in the lowland rain-forest and include no Musci.

(iv) *Community on rotten logs*. This has a very similar composition to (ii).

(v) *Ground flora*. The growth of woody plants is so dense as to leave little room for anything else, but here and there are patches of bare humus, water-logged even in the driest weather. Here are found thin carpets of *Sphagnum*

*Beccarii* and *S. sericeum* (both absent in the shadier parts), also *Mniodendron divaricatum*, *M. microloma*, *Leucobryum sanctum*, and (rarely) *Acroporium* spp. In this habitat hepatics are almost absent.

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*List of some abbreviations.*

<i>Abbreviation.</i>	<i>Full designation.</i>
Dulit ; L. C. Dulit . . . . .	Near Long Kapa, Mount Dulit (Ulu Tinjar). IVth Division. (Refers to the neighbourhood of the Expedition's Base Camp.)
Bank of R. Tinjar, Dulit. . . . .	Bank of River Tinjar, near Mt. Dulit. IVth Division.
Dulit Ridge . . . . .	Crest of Mt. Dulit (Ulu Tinjar). IVth Division. (Refers to the neighbourhood of the Expedition's High Camp.)
Dulit Trail . . . . .	Mount Dulit (Ulu Tinjar). IVth Division. (Refers to the path connecting the Base Camp and High Camp.)
Ulu Koyan . . . . .	Slopes of Mt. Dulit drained by the Koyan River (Rejang Basin). IIIrd Division.
S. Balapau . . . . .	Balapau River (Ulu Tinjar). IVth Division.
G. Laiun, S. Balapau . . . . .	Mt. Laiun, Balapau River (Tinjar-Baram Water- shed). IVth Division.
Mt. Mulu . . . . .	Mount Mulu. IVth Division.
Marudi . . . . .	Marudi (or Claudetown). IVth Division.
Miri . . . . .	Miri. IVth Division.
Niah . . . . .	Niah. IVth Division.
G. Santubong . . . . .	Santubong Mountain. Ist Division.
Bidi Cave . . . . .	Bidi Cave, Ulu Sarawak. Ist Division.

G.=Gunong (Mountain).

S.=Sungei (River).

## SPHAGNACEAE.

## SPHAGNUM BECCARII Hampe

On ground in open moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 9 Oct. 1932; coll. Oxford Exped. (2179, 2184).

## SPHAGNUM SERICEUM C. M.

Maraparai Ridge, c. 1,500 m., Brit. N. Borneo, 24 Nov. 1931; coll. Holttum (25622). On ground in shady moss forest, c. 1,400 m., Dulit Ridge, Sarawak, 8 Oct. 1932; coll. Oxford Exped. (2185).

New to Borneo. *Distr.* Sumatra; Java; Philippines; Malay Penins.

## SPHAGNUM CUSPIDATULUM C. M.

Lumu-Lumu, Kamborangah, 1,600–2,200 m., Brit. N. Borneo, 13 Nov. 1931; coll. Holttum (25463).

New to Borneo. *Distr.* Malay Penins.; Siam; India; Celebes; Philippines.

## SPHAGNUM SUBRECOURVUM Warnst. var. nov. BORNEËNSE Dix.

A forma typica differt statura minore, foliorum caulinorum limbo inferne paullo dilatato, poris foliorum rameorum superficie ventrali paucis vel nullis.

*Hab.* Sandstone rocks in river bed, c. 800 m., Ulu Koyan, Sarawak, 22 Sept. 1932; coll. Oxford Exped. (2045).

The species is new to Borneo. *Distr.* Java; Siam.

A very small plant, which differs slightly from the Javan form. In that the border of the stem leaves is not widened below; here it is slightly but distinctly widened; I also find no pores on the ventral surface of the branch leaves, which there are described as present. I have thought it best to describe it as a var. of the Javan plant, but it may be a distinct species.

## SPHAGNUM JUNGHUHNIANUM Doz. &amp; Molk.

Below Pakka, c. 1,300 m., Kinabalu, 15 Nov. 1931; coll. Holttum (25341). Lumu-Lumu, Kamborangah, 1,700–2,200 m., Brit. N. Borneo, 13 Nov. 1931; coll. Holttum (25466), forma compacta. Foot of trees in dwarf forest, c. 900 m., G. Santubong, Sarawak, Dec. 1932; coll. Oxford Exped. (2730).

New to Borneo. *Distr.* Himalayas; Yunnan; Japan; Formosa; Philippines; Celebes; Java.

## ANDREAEACEAE.

## ANDREAEA KINABALUENSIS Dix., sp. n. (Pl. 1, fig. 1.)

Eu-Andreaea. §Nerviae.

*A. rigidæ* Wils. himalayanae affinis. Folia paullo breviora, minus fortiter circinnata; e basi breviora, magis ovata, magis raptim in subulam angustata. Costa male limitata; cellulae inferiores magis elongatae, versus basin atque costam sensim longiores, infimae juxtacostales plures lineares. Bractee perichaetii sat longe, acute cuspidatae.

*Hab.* Pakka, 3,110 m., Kinabalu, 15 Nov. 1931 ; coll. Holttum (25187 b).

Near to *A. rigida*, forming deep, loose, blackish tufts, some 3 cm. high. It has the leaves somewhat less strongly falcate, but they vary much in that respect in both plants. The leaf-base in the Himalayan species is more lanceolate, more gradually tapering into the subula, and therefore occupying a larger proportion of the leaf. The nerve in *A. rigida* is clearly defined below, while in the present plant it is ill-defined ; this is in part due to the juxtacostal cells, which in this are more or less elongate, and therefore similar to those of the nerve ; while in *A. rigida* the small isodiametrical cells are continued almost unaltered to the base and to the nerve.

It forms an interesting extension of the range of the genus. The Asiatic distribution of *Andreaea* appears to be as follows :—Himalayas, five species (including one unpublished species in my herbarium from E. Tibet) ; Japan, one species ; Amur, one species ; Tchutschican Peninsula, five spp. It is, however, highly probable that several at least of the last six species will ultimately be reduced to *A. petrophila*.

#### DICRANACEAE.

WILSONIELLA TONKINENSIS Besch.

Clay banks of road, Marudi, Baram, Sarawak, 25 July 1932 ; coll. Oxford Exped. (1003).

WILSONIELLA PELLUCIDA (Wils.) C. M. var. nov. ACUTIFOLIA (Broth.) Dix.

Folia longiora, angustiora, apice *acuminato*, *peracuto*.

Tayabas, Luzon, Philippines, May 1917 ; coll. Ramos and Edanc (28940). Herb. Brotherus, type. Gua Batu, Selangor, 1896 ; coll. Ridley (481). Hayoep, S.E. Borneo, 16 June 1908 ; coll. Hubert Winkler ; Herb. Kew (2520).

The specimen from Brotherus's Herbarium is labelled in Brotherus's hand 'Wilsonianella acutifolia Broth.' So far as I can ascertain the name is unpublished. It differs very markedly from the type (especially as figured by Fleischer) in the longer, very narrow, and very narrowly acuminate leaves. The fruiting characters appear identical. I have, however, seen leaves of *W. pellucida* from India approaching this form, and I think it is best treated as a variety.

In the 'Musci', ed. ii, Brotherus lists a *W. bornensis* Broth., but I believe this too has not been published ; and I have not been able to see a specimen of it, so that I am unable to say whether it is the present plant or not.

DITRICHUM SPINULOSUM Dix., sp. n. (Pl. 1, fig. 2.)

Robustum, habitu *D. flexicaulis*. Ab eo differt foliis e basi *breviore*, supra *magis sensim angustata*, *rigidioribus*, subula omnino *laevi*, versus apicem *distanter*, *fortiter spinuloso-dentata*. Foliorum subula sicca nitida, pulchre spiraliter contorta. Fructus haud visus.

*Hab.* Pakka, 3,110 m., Kinabalu, 15 Nov. 1931 ; coll. Holttum (25187), type. Idem, 3,660 m., Kinabalu (C). Ibidem, 4,080 m. (G).

The type is a dark olive-green, the other two numbers yellowish green. The plant is in habit much like the more robust forms of *D. flexicaule*, but the cells of the sheathing part of the leaf are linear and quite different. In the glossy, spirally twisted subula the species resembles *D. spirale* Dix. from S. Africa, as well as in the strongly spinulose toothing of the apex ; but that species has shorter leaves, and the sheathing base much more gradually attenuated above.

*MICRODUS MIQUELIANUS* (Mont.) Besch.

. Mud of river bank, under 300 m., G. Dulit, Sarawak, 13 Aug. 1932 ; coll. Oxford Exped. (1234).

*MICRODUS MACROMORPHUS* Fleisch.

On soil on crest of spur, c. 400 m., Dulit Trail, Sarawak, 27 Aug. 1932 ; coll. Oxford Exped. (1508).

Fleischer bases his species on the large size, the seta dark red (not yellowish above), the peristome teeth often split to the base. The present plant is a very small one, but the seta is purple-red and the teeth are mostly split. I doubt the value of the species, but if it be maintained it should be on the ground of its structural characters rather than on its size, and the present plant should therefore be referred to it.

*DICRANELLA SETIFERA* (Mitt.) Jaeg. (*D. tenuifolia* (C. M.) Fleisch.).

Between Dallas and Tenompok, 900–1,400 m., Brit. N. Borneo, 7 Nov. 1931 ; coll. Holttum (25354).

New to Borneo. *Distr.* Sikkim ; Assam ; Sumatra ; Java ; Philippines.

According to Fleischer's description, *D. tenuifolia* should differ from *D. setifera* in the capsule 'fast glatt' ; but in Fleischer's own specimen (M. Fr. Arch. Ind. 118) the capsules are quite distinctly furrowed. I can find no other difference.

C. Müller's species and Mitten's were both published in 1859. As Mitten's paper was read in May 1858, I think it may be presumed that his was the earlier publication.

*BRAUNFELSIA PLICATA* (Lac.) Fleisch.

On upper part of trunk of large felled tree in rain-forest, Dulit Trail, Sarawak, 9 Aug. 1932 ; coll. Oxford Exped. (1184).

New to Borneo. *Distr.* Malay Penins. ; Java ; Celebes.

*BRAUNFELSIA SCARIOSA* (Wils.) Par. (*B. involuta* (Lac.) Fleisch.).

On rock in low open forest, near Pakka, Kinabalu, 3,100 m., 15 Nov. 1931 ; coll. Holttum (25649, 25667).

No. 25649 has the leaves sometimes quite nerveless, sometimes with a fairly strong nerve reaching to mid-leaf ; this diversity being sometimes shown by leaves taken from the same stem, and almost from the same point on the stem. No. 25667 has very finely subulate, almost hair-pointed leaves, with long

setae, up to almost 2 cm., much exceeding the perichaetial leaves. In view of this variability, especially in the presence or absence of the nerve, I think there is no doubt that *B. involuta* is simply a nerveless form of this species, and in all probability *B. papuana* Reim. is also the same. I have found much variation in *B. scariosa* as to the length of the leaf-point and the height of the seta, which may be shorter than the perichaetial leaves or may considerably exceed them.

*BRAUNFELSIA LONGIPES* Dix. (*B. latifolia* Broth.).

Tree-trunk in open moss forest, near ground, 1,230–1,400 m., Dulit Ridge, Sarawak, 5 Oct. 1932; coll. Oxford Exped. (1932, 2146).

The seta here is slightly shorter than in the original plant, but the broad leaves are characteristic. Brotherus's plant is identical with mine, but the name was published four years later.

*DICRANOLOMA BLUMII* (Nees) Par.

Lumu-Lumu, 1,500 m., Kinabalu, 18 June, 1925; coll. C. M. Enriquez (18142). Ibidem, 12 Dec. 1931; coll. Holttum (25634). Kemoel, W. Koetai, Oct. 1925; coll. F. H. Endert (4516 p.p.), Herb. Hort. Bot. Bog. (2552), c.fr. G. Rumpit, Sarawak; coll. J. W. Anderson, Herb. Singapore Bot. Gard. (186), c.fr.

*DICRANOLOMA BRAUNII* (C. M.) Par.

Kamborangah, Brit. N. Borneo, 17 Nov. 1931; coll. Holttum (J.).

*DICRANOLOMA ASSIMILE* (Hampe) Par.

Kemoel, W. Koetai, Oct. 1925; coll. F. H. Endert (4516 p.p.), Herb. Hort. Bot. Bog. (2552 b). A slender form.

*DICRANOLOMA SUBECOSTATUM* Dix., nom. nov. (*D. subenerve* Broth., 1928; nec *D. subenerve* Herz., 1925).

Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931; coll. Holttum (25195). Between Lumu-Lumu and Kamborangah, 1,700–2,200 m., 13 Nov. 1931; coll. Holttum (25640).

Brotherus's name was pre-occupied for a Brazilian moss, published by Herzog in 1925.

*DICRANOLOMA EURYLOMA* Dix., sp. n.

Sat robustum; habitu *D. reflexifolii*. Folia horride patentia, ramorum apicibus saepe leniter falcato-secunda, circa 7 mm. longa, e basi ovato-lanceolata sat breviter subulata, haud plicata, versus apicem fortiter spinose dentata. Costa angustiuscula, inferne circa 60  $\mu$  lata, percurrent, dorso superne ad medium fere folium argute spinoso-serrata. Areolatio valde tenuis, pellucida, confluent, cellulae omnes subsimiles, breviter lineari-rhomboideae, subsigmoideae, apicibus rotundatis, superiores breviores, circa 4–5  $\times$  1, parietibus tenuibus, porosis. Cellulae marginales hyalinae, pluri-seriatae (usque 8), limbum pernotatum, usque ad 120–150  $\mu$  latum, longe supra medium folium

attingentem formantes. Perichaetium longum, 1 cm. vel ultra, bracteis pallidis convolutis, in subulam longam setaceam *denticulatam* flexuosam abrupte contractis. Setae aggregatae, immaturae ad 1.5 cm. longae, tenues; thecae immaturae solum visae.

*Hab.* Lumu-Lumu, alt. 1,400–1,600 m., Tenompok, Brit. N. Borneo, 12 Nov. 1931; coll. Holttum (25633), type. At base of tree in white sand forest, c. 1,000 m., 15 Sept. 1932; coll. Oxford Exped. (1853).

A very distinct species, in its leaf structure much resembling the Australasian *D. fasciatum* (Hedw.), especially in the strong border, reaching high in the leaf—in fact, to where the serratures begin. The toothing is very strong, that of the back of the nerve reaching considerably lower in the leaf than the marginal serratures. The cells are exceedingly thin, and the wall narrow and similar in colour to the lumen, so that the areolation is remarkably ‘confluent’.

*DICRANOLOMA ANGUSTIFRONDEUM* Dix., sp. n. (Pl. 1, fig. 3.)

Elatum; ad 14 cm. altum; caules subgracilescentes, flexuosi, parum ramosi, dense brevissime albide tomentosi, fusco-aurantiaci. Folia parum conferta, erecto-patentia, breviuscula, frondem *angustiusculam*, vix 5 mm. latam sistentia. Folia 5–6 mm. longa, e basi *brevissima* orbiculari-cordata, raptim in laminam *latam, strictam*, sensim in acumen *latiusculum* acutum, nec subulatum, *acute carinatum*, angustata, basin versus denticulata, supra magis fortiter, *densissime, spinulose dentata*. Costa validiuscula, e basi fere carinata, dorso ab apice usque ad longe infra medium folium seriebus duabus dense fortiter dentata. Areolatio viridis, *laxiuscula*, e cellulis omnibus elongatis, linearibus, supra lineari-rhomboides, latiusculis, parietibus incrassatis, porosis, sed valde pellucidis, instructa. Fructus ignotus.

*Hab.* Tenompok, on tree, 1,220 m., Brit. N. Borneo, 17 June 1925; coll. C. M. Enriquez (18,111).

A very marked species. The comparatively distant leaves, with a *very short*, divaricate, glossy leaf-base suddenly narrowed into the more erect narrow lamina, give a curiously catenulate appearance to the stems. The lamina is wide and broadly pointed, deeply carinate and coarsely toothed at back from near the base, with the margins also densely and strongly toothed. The cells are comparatively wide, rather obscure with the primordial utricle, and chlorophyllose.

*DICRANOLOMA PERINTEGNUM* Dix.

On tree-trunk in moss forest, c. 1,300 m., Dulit Ridge, Sarawak, 6 Oct. 1932; coll. Oxford Exped. (2167).

New to Borneo. *Distr.* Malay Penins.

*LEUCOLOMA MOLLE* (C. M.) Mitt.

Between Tenompok and Lumu-Lumu, 1,450–1,700 m., Brit. N. Borneo, 12 Nov. 1931; coll. Holttum (25691), f. *elata*.

New to Borneo. *Distr.* Wide in Indo-Malaya, &c., from New Guinea to Japan and China.

**CAMPYLOPUS SERICEOIDES** Dix., sp. n.§ **Pseudo-Campylopus.**

*C. sericeo* Fleisch. affinis; robustior, subnitens, *rigidus*, *olivaceo-viridis*; caules *haud tomentosi*; folia laxiora, *majora*, 10–12 mm. longa, e basi latiore, *minus concava* sensim subulata, integra, summo apice tantum parce denticulato. Costa *latissima*, prope basin 0.45–0.5 mm. lata, sectione eae *C. sericei* similis. Cellulae alares plus minusve notatae, supra-ales ut in *C. sericeo*, superiores omnes, et laminae et costae dorso, *minutae*, *breviter rectangulares vel rhomboideae*. Fructus ignotus.

*Hab.* Pakka, 3,100 m., Kinabalu, 15 Nov. 1931; coll. Holttum (25189), type. Kinabalu, alt. 4,080 m., 14 Nov. 1931; coll. Holttum (F).

A species of the Pseudo-Campylopus group, nearest to *C. sericeus* Fl., but that is a paler, softer, smaller plant, with tomentose stems, the leaves very concave-convolute from the base, with a rather narrower nerve, and with the upper cells all elongate. Here in the upper part of the leaf they are all small and short, covering the back of the nerve, as well as the lamina.

The nerve section in 25189 is fairly typical of the Pseudo-Campylopus type, the dorsal layers of cells consisting mostly of substereids. The ventral cells are large and empty, the guide-cells rather smaller, but empty and conspicuous. In (F), however, the nerve section is very peculiar and indeed abnormal, the dorsal cells being sometimes quite large—in fact, at times the section shows three layers of subequal lax cells, and is very similar to that of *Paraleucobryum*, while at other times the cells are very irregular and variable in size and position, occasionally showing a row of small empty cells between the ventral layer and the guide cells.

The alar cells are extremely variable, often scarcely differentiated, at other times forming widened, very distinct, coloured auricles. The subula of the leaf also varies greatly, being sometimes long, fine, quite entire to the tip, or there with one or two teeth; at others shorter, broader, subobtusate, with the apex more strongly denticulate.

**CAMPYLOPUS AUREUS** Bry. jav.

Among *Agrostis*, Upper Kinabalu, c. 3,960 m., 1932; coll. J. & M. S. Clemens, Herb. Hort. Bot. Bog. (2949 b). Kinabalu, c. 2,750 m., 14 Nov. 1931; coll. Holttum (25661). Holttum's plant has longish white hair-points and large auricles, but in general agrees with *C. aureus*; no. 2949 b is almost without the hair-point, but otherwise agrees and confirms the identification. I have an almost similar form from Java.

New to Borneo. *Distr.* Ceylon; South India; Nicobar Is.; Java; Celebes; New Guinea.

**CAMPYLOPUS SERRATUS** Lac.

Miri, Baram, Sarawak, 23 Apr. 1895; coll. Chas. Hose, Herb. Kew. (738). Borneo, loco incerto, 1913; coll. Wegner, Herb. Herzog (6). Mandarbosch,



Pontianak, Dec. 1930 ; coll. Dr. E. Polak (201), Herb. Hort. Bot. Bog. (2594). Sandy banks in clearing, Marudi, Baram, 25 July 1932 ; coll. Oxford Exped. (1017).

New to Borneo. *Distr.* Banca ; Malay Penins. ; Siam.

*CAMPYLOPUS (THYSANOMITRIUM) EXASPERATUS* Brid.

Kinabalu, c. 2,750 m., 16 Nov. 1931 ; coll. Holttum (25670).

*CAMPYLOPUS (THYSANOMITRIUM) UMBELLATUS* W.-Arn.

Kinabalu, c. 2,750 m., 16 Nov. 1931 ; coll. Holttum (25674). Dallas, Brit. N. Borneo, c. 900 m., 5 Nov. 1931 ; coll. Holttum (25255). Sandstone rocks in spray by waterfall, c. 1,200 m., Dulit Ridge, Sarawak, 14 Sept. 1932 ; coll. Oxford Exped. (1915). A form with very long, fine, almost leafless, floriferous prolongations of the stems, reaching over 6 cm. in height. In similar situation, 12 Sept. 1932 ; coll. Oxford Exped. (1756).

*DICRANODONTIUM NITIDUM* (Bry. jav.) Fleisch.

Kinabalu, c. 2,600 m., 16 Nov. 1931 ; coll. Holttum (25664). A form with leaves rather narrow below, and the basal cells very porose.

#### LEUCOBRYACEAE.

*SCHISTOMITRIUM ROBUSTUM* Doz. & Molk.

Liang gagang, Borneo ; coll. H. Hallier, Borneo-Exped., 1893-4 ; Herb. Hort. Bot. Bog. (2955), c.fr.

New to Borneo. Hitherto known from three localities in Java only.

*SCHISTOMITRIUM LOWII* Mitt.

Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931 ; coll. Holttum (25660).

*SCHISTOMITRIUM APICULATUM* Doz. & Molk.

Bolset, W. Koetai, Aug. 1925 ; coll. F. H. Endert, Herb. Hort. Bot. Bog. (2508). On tree in moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 19 Sept. 1932 ; coll. Oxford Exped. (1942). On fallen tree-trunk, c. 800 m., Ulu Koyan, Sarawak, 22 Sept. 1932 ; coll. Oxford Exped. (2034).

*SCHISTOMITRIUM COPELANDII* Broth.

On tree in white sand forest, c. 1,000 m., Ulu Koyan, G. Dulit, 15 Sept. 1932 ; coll. Oxford Exped. (1854, 1861).

New to Borneo. *Distr.* Philippines ; Malay Penins.

The geographical distribution of this genus is interesting. Ten species have been described, of which three belong to New Guinea, five are found in Borneo, three in Java, four in the Philippines, and one, *S. apiculatum*, which has the widest distribution of all, is found in Sumatra, Java, Borneo, and the Philippines. Only one is known from Continental Asia.

## CLADOPODANTHUS DOZ. &amp; MOLK.

This genus was founded for *Leucobryum piliferum* Jaeg., principally on the 'cladogenous' position of the fruit, the stem being supposed to be prostrate, with the fruit produced on short lateral branches; but Fleischer has pointed out that this is exceptional; the outer stems of a tuft may be prostrate, while the central ones are erect; and the fruit is produced laterally, on very short lateral fruiting branches. The normal branching, in fact, appears to be dichotomous or fastigiate.

Fleischer has brought *Spirula speciosa* Doz. & Molk. also into this genus, where it clearly belongs. The fruit, however, is not always produced laterally as Fleischer figures it; in specimens from both Borneo and Celebes I find the perichaetia produced practically at the apex of the normal branch, which, however, at once continues to grow beyond it, so that the perichaetium becomes lateral. In the two new species described below, however, the fruit is clearly terminal, and it becomes a question whether these should be placed in a new genus or whether the 'cladogenous' character should be considered of minor importance. The peristome appears to give no good character, and I think the genus must be based mainly on the calyptra, which is similar to that of *Schistomitrium*, but not fringed at the base—either entire or very faintly notched; the nerve-structure shows no marked characters.

The genus, of four species only, is a very remarkable one, both in habit and foliation, and in its distribution. *C. pilifer* has hitherto been known from two localities only in Java, but it was collected by G. A. C. Herklots on Fraser Hill, Pahang, Malay Penins., in June 1929. *C. speciosus* is recorded by Fleischer from three localities in Java, and was not known elsewhere; I have it, however, from Celebes, where it was collected by Kjellberg in 1929, as well as from Borneo as given below. Both these fine species have a very striking and peculiar foliation. Finally, the two new species described below are, so far, endemic to Borneo, and the leaf in *C. truncatus* is of a form unique among the mosses.

## CLADOPODANTHUS SPECIOSUS (Doz. &amp; Molk.) Fleisch.

Trunk of tree, 6 m. from ground, in moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 5 Oct. 1932; coll. Oxford Exped. (2137). In tall dense tufts, richly fruiting, the fruit often produced from the apices of the branches. On rotten branches recently fallen in shady moss forest, c. 1,300 m., Dulit Ridge, Sarawak, 17 Sept. 1932; coll. Oxford Exped. (1901). Sterile.

New to Borneo. *Distr.* Java; Celebes.

## CLADOPODANTHUS TRUNCATUS Dix., sp. n. (Pl. 1, fig. 6).

Densissime caespitosus, humilis, 2 cm. altus, pallide stramineus, infra fuscus, dense ramosus, ramis brevibus, turgidis, obtusis. Folia densissime conferta, suberecta, sicca vix mutata, erecto-appressa, stricta, oblonga, 2.5 mm. longa, 5 mm. lata, perconcaeva, apicem versus subtubulosa; folii apex late truncatus,

summitate aut exacte horizontali aut leniter emarginata, unde apex leniter bicornuta fit. Limbus folii (lamina vera) fere nullus, perangustus, e cellulis 1-2-seriatis angustissimis, parietibus tenuibus interrupte valde porosis, instructus, male definitus, infra medium folium solutus; margines integerrimi. Cellulae basilares ad insertionem vix angustatam aurantiacae.

Costa sectione subhomostrosica, leucocystibus paucis prope basin, praecipue ventralibus, hic illic transverse divisus; cellulae chlorophyllosae ibi subcentrales; supra magis hypocentricae, supra medium folium valde hypocentricae unde leucocystes dorsales multo minores quam ventrales. Perichaetia apicibus ramorum terminalia, bracteis foliis caulinis subsimilibus, superne breviter angustatis, acutis. Seta ut videtur perbrevis, vix 5 mm., tenuis. Calyptra conico-mitriiformis, basi haud vel vix fissa, subintegra, non laciniata.

*Hab.* Rotten trunk and earth in 'heath forest', under 300 m., Forest Reserve, Marudi, Sarawak, Nov. 1932; coll. Oxford Exped. (2675).

A remarkable plant, differing in the truncate leaves from any moss that I know, with the possible exception of one or two species of *Glossadelphus*. The line across the apex may be quite straight, as if cut square across with a knife, or more frequently it is slightly concave, so that the angles shortly project in two small horns, while there is occasionally a short median apiculus as well. The figures will give a better idea of this than a description can do.

The single tuft gathered is fruiting freely, but the fruit was unfortunately quite immature. The seta, however, has probably attained almost its full length, and the calyptra is sufficiently developed to make it practically certain that it is of the type of *Cladopodanthus*, not fringed as in *Schistomitrium*.

*CLADOPODANTHUS MICROCARPUS* Dix., sp. n. (Pl. 1, fig. 5.)

E minoribus speciebus. Humilis, perdense compactus, albescens. Caules dense ramosi, ramis brevibus, nunc obtusis, nunc breviter cuspidatis. Folia dense conferta, aut erecto-patentia aut falcato-secunda, rigida, sicca haud mutata, circa 2.5 mm. longa, perconcava, e basi oblonga breviter, late, stricte acuminata, sensim breviter cuspidata, integerrima. Costa sectione subhomostrosica, leucocystibus perpauca ventralibus prope infimam basin transverse septatis; cellulae chlorophyllosae subcentricae vel hypocentricae, supra fortiter hypocentricae, apicem versus leucocystibus ventralibus multo majoribus, haud divisis. Limbus folii angustissimus, vix evolutus.

Fructus terminalis; bractee perichaetii breviores, latiores quam folia caulina; seta perbrevis, 4-5 mm. tantum longa, saturate rubra; theca minuta, elliptica, suburceolata, collo defluente, deoperculata circa 0.5 mm. longa. Peristomium fuscum, dentes ad basin connati fere, integri, arcte lamellati, ubique dense papilloso. Operculum recte aciculari-rostratum. Calyptra mitriiformis, ad basin ut videtur haud ciliata, brevissime eroso-laciniata.

*Hab.* On fallen tree-trunk, c. 800 m., Ulu Koyan, Sarawak, 22 Sept. 1932; coll. Oxford Exped. (2034 bis).

A small species, which I was at first inclined to put into *Schistomitrium*,

the leaf form being much more of that genus than any of the known species of *Cladopodanthus*. The leaf-structure, however, is almost exactly that of *C. truncatus*, the habit is similar, the stems on the outside of the tufts being more or less prostrate, with erect lateral branches, and the calyptra is not fringed at the base—in fact, almost entire. The capsule is smaller and shorter than in any species of either of the two genera.

In habit it is very like *S. apiculatum* Doz. & Molk., but that species has the leaves somewhat rapidly contracted above the base into a longer subflexuose acumen, terminated more abruptly in a slightly curved apiculus. Here the leaves are *gradually* narrowed from somewhat above the base to a quite straight, acute, rigid point.

**LEUCOBRYUM SANCTUM (Brid.) Hampe**

A common species in Borneo. A rather remarkable form was collected by the Oxford Expedition on sandy ground by a streamlet in moss forest, c. 1,230 m., on Dulit Ridge (2202), with very turgid stems, the leaves densely crowded and very long.

**LEUCOBRYUM SCALARE C. M.**

On ground in sandy forest, c. 800 m., 15 Sept. 1932; coll. Oxford Exped. (1848).

**LEUCOBRYUM ADUNCUM Doz. & Molk.**

On ground on edge of cliff, 1,230 m., Dulit Ridge, Sarawak, 19 Sept. 1932; coll. Oxford Exped. (1976).

**LEUCOBRYUM BOWRINGII Mitt.**

G. Dulit, Sarawak, 1932; coll. Oxford Exped. (1757)

**LEUCOBRYUM JAVENSE (Brid.) Mitt.**

From numerous localities.

**LEUCOBRYUM PULCHRUM Broth. (syn. *L. sumatranum* Broth.).**

This species was published by me (as *L. sumatranum* Broth.) in Ann. Bryol. v, 24 (1932), founded on Brotherus's type from Sumatra—an original specimen sent me by Brotherus at an earlier date. Recently I discovered that under the name *L. pulchrum* Brotherus had already published this species, founded on a Borneo moss—either having forgotten his MS. name for the Sumatran plant or, more probably, not having detected the identity of the two plants.

**LEUCOBRYUM PENTASTICHUM Doz. & Molk.**

From inside a monkey skin, sent to the British Museum from Baram, coll. Bishop Hose.

This agrees with Javan specimens (Fleischer, M. Fr. Arch. Ind. 53); but I confess I find it very difficult to separate from *L. Teyssmannianum*, and both from the Australasian *L. candidum* var. *speirostichum* (C. M.).

**LEUCOPHANES CANDIDUM** (Hornsch.) Lindb. (*L. densifolium* Mitt.).

Collected by the Oxford Exped. in several localities. On tree-trunk, Marudi, Baram, 25 July 1932 (1022). Heath-forest, under 300 m., Forest Reserve, Marudi, Nov. 1932 (2665). Under 300 m. Niah, Sarawak, Nov. 1932 (2706).

Fleischer has pointed out the close relationship of *L. densifolium* to this plant, under which he places it (but as a subspecies). Some of the plants above, however, make it clear that even that position cannot be upheld; no. 2665 is a form intermediate between the two, while 2706 shows, in the same gathering, a transition of forms from absolutely typical *L. candidum* to *L. densifolium*. The habit and often the colour are so different that it is difficult to realize that they are conspecific. I can myself see no difference from the 'densifolium' form in *L. aciculare* C. M. (ined.).

**LEUCOPHANES ALBESCENS** C. M.

Hayoep, South-east Borneo; coll. Hubert Winkler, Herb. Kew. (2446).

**EXODICTYON BLUMII** (C. M.) Fleisch.

Bettotan, near Sandakan, 25 Jan. 1927; coll. C. Boden Kloss (189733 A).

**FISSIDENTACEAE.****FISSIDENS VIRENS** Mitt. (*F. asperifolius* Broth. & Fleisch.).

On termites' nest at base of tree, under 300 m., G. Dulit, Sarawak, 2 Sept. 1932; coll. Oxford Exped. (1606).

New to Borneo. *Distr.* Ceylon; Java (as *F. asperifolius*).

I have compared the Javan plant with the original of *F. virens*, and can find no difference at all. According to Fleischer, the Ceylon moss has narrower leaves, incurved when moist as well as when dry, with longer papillae, the lid equal in length to the capsule, and a smaller habit. I can find no difference in any of these characters. In both the Javan and the Ceylonese moss the lid varies from about equalling to being considerably shorter than the capsule. The leaves are distinctly, though not strongly, undulate when moist.

**FISSIDENS LONGEVAGINATUS** Dix., sp. n. (Pl. 1, fig. 7.)§ *Semilimbium*.

Caules longiusculi, circa 5 mm. longi, laxe caespitosi, sordide virides; folia sicca leniter decurvo-falcata, confertiuscula, circa 1.5 mm. longa, 0.4 mm. lata, late oblonga, haud acuminata, late rotundata, apice vel omnino obtuso vel minute obtuse apiculato; integra vel obscure crenulata. Costa validiuscula, concolor, percurrent. Lamina vaginans praelonga, ad  $\frac{3}{4}$  folii longitudinis attingens. Lamina dorsalis ad basin costae sensim desinens. Lamina vaginans tantum limbata, limbidio sat valido subincrassato, flavescente. Areolatio pellucida, e cellulis 8–11  $\mu$  latis, irregulariter hexagonis, dense, humiliter papillosis, limitibus firmis, distinctis, instructa.

Heteroica. Antheridia aut nuda aut bracteata, foliorum axillis caulis

fertilis. Fructus terminalis, seta circa 4 mm. alta; theca erecta, minuta, sicca urceolata; peristomium intense purpureum, dentibus intus alte lamellatis, haud papillosis.

*Hab.* Muddy bank of river, liable to flooding, R. Tinjar, G. Dulit, Sarawak, under 300 m., 23 Aug. 1932; coll. Oxford Exped. (1425).

A well-marked species, in the unusually long vaginant lamina with rather strong limbidium, the broadly rounded apex of the leaf, and distinct pellucid areolation. The ♂ flowers are certainly at times axillary on the fertile stems, but I think may be also on separate stems; naked antheridia also sometimes occur in axillary groups below the female inflorescence.

*FISSIDENS ALBO-LIMBATUS* Dix., sp. n. (Pl. 1, fig. 8.)

§ *Semilimbium*.

Pusillus; caules tantum 2-3 mm. longi, laxe caespitosi, plumose foliosi, foliis siccis leniter falcatis, confertiusculis, circa 1.5 mm. longis, 0.2 mm. latis, anguste oblongo-lanceolatis, peracutis, marginibus integris. Lamina vaginans praelonga, usque ad  $\frac{3}{4}$  folii longitudinem vel ultra; limbidio lato, albo praedita. Costa angusta, hyalina, subpercurrent, infra apicem saepe geniculata. Cellulae minutissimae, perobscurae, peropacae. Dioicum videtur. Fructus haud visus, solum archegonia terminalia.

*Hab.* Shaded moist rocks on mountain, c. 850 m., in pale green, later yellow patches, Dulit Trail, Sarawak, 31 Aug. 1932; coll. Oxford Exped. (1587).

To be compared with *F. ceylonensis* Doz. & Molk., which, as Fleischer remarks, has an almost uniquely opaque and obscure areolation, 'as in no other species'. It is, perhaps, outdone in this respect by the present plant, and the effect is enhanced by the highly pellucid, hyaline nerve and border. From that species it differs at once in the very acute leaves and the long vaginant lamina. The latter character, but no other, is shared with the preceding species.

*FISSIDENS CRASSINERVIS* Lac.

Moist sandstone rocks, c. 800 m., Ulu Koyan, Sarawak, 22 Sept. 1932; coll. Oxford Exped. (2040). Bare soil in rain-forest on steep ridge, under 300 m.. G. Dulit, Sarawak; coll. Oxford Exped. (1141).

Shows considerable diversity in the form of the leaves, which may be exceedingly finely and acutely acuminate. No. 2040 is a very pretty plant, with stems 1.5 cm. high, strict, and regularly plumose.

*FISSIDENS PAPILLOSUS* Lac.

Calcareous soil in cave, under 300 m., Bidi, Sarawak, Dec. 1932; coll. Oxford Exped. (2753).

New to Borneo. *Distr.* Java.

Recorded by Fleischer from a single locality only in Java, but I have it also from that island from G. Semeroe, Res. Pasoertoean, 800-1,200 m., June 1930; coll. Fr. Verdoorn. In both cases it was corticolous. The Borneo plant is identical.

**FISSIDENS PUNCTULATUS** Lac.

Lobang, 1,225 m., Brit. N. Borneo, 19 Nov. 1931; coll. Holttum (25686). On bark of tree in secondary forest, on river-bank, under 300 m., G. Dulit, Sarawak; coll. Oxford Exped. (1286).

**FISSIDENS SYLVATICUS** Griff. (*F. Zippelianus* Doz. & Molk.).

Moist sandstone rocks by waterfall, c. 1,100 m., Dulit Ridge, Sarawak, Sept. 1932; coll. Oxford Exped. (2194). A form with narrow, often acuminate leaves. The species was also collected with other mosses in one or two localities.

**FISSIDENS JAVANICUS** Doz. & Molk.

Wet rocks in stream-bed, under 300 m., G. Dulit, Sarawak, 2 Sept. 1932; coll. Oxford Exped. (1607).

New to Borneo. *Distr.* Java; Sumatra; Andaman Is.; Malay Penins.; Siam; Assam; Himalayas.

**FISSIDENS NOBILIS** Griff.

Below Dallas, c. 900 m., Brit. N. Borneo, 6 Nov. 1931; coll. Holttum (25282). Kinabalu, c. 1,500 m.; coll. J. & M. S. Clemens (34144).

**FISSIDENS PERPELLUCIDUS** Dix., sp. n. (Pl. 1, fig. 9.)**Serridium?**

*Elatus*, gregarius, *nitidus*, *flavescens*. Caules ad 2 cm. alti, percomplanati, 4–5 mm. lati. Folia laxiuscule disposita, sicca leniter flexuosa, 3 mm. vel paullo ultra longa, 0.5 mm. lata, lingulata, *breviter acuta*, vel *inaequaliter, raptim apiculata*, plerumque integra. Lamina vaginans multo minus quam dimidiam partem folii attingens, media folii lamina terminata. Costa validiuscula, concolor, pellucida, supra sensim angustata, *paullo infra apicem soluta*, ad apicem laminae vaginantis geniculata. Areolatio *perpellucida*, e cellulis rotundato-hexagonis, irregularibus, *valde incrassatis*, 10–12  $\mu$  latis, laevibus, versus basin vix majoribus, instructa.

Dioicum. Archegonia terminalia tantum visa.

*Hab.* At c. 900 m. alt., 39th mile from Dallas, Brit. N. Borneo, 5 Nov. 1931; coll. Holttum (25265), type. Moist rocks in primary forest, spur of mountain, c. 700 m., Dulit Trail, Sarawak, 27 Aug. 1932; coll. Oxford Exped. (1506). Shaded moist rocks, c. 850 m., Dulit Trail, Sarawak, 31 Aug. 1932; coll. Oxford Exped. (1586 b, 1589).

A distinct species, the position of which is uncertain. In the glossy pellucid leaves (little altered when dry), the areolation, the terminal inflorescence, it suggests *Aloma*. None of these characters is inconsistent, however, with *Serridium*, while the size of the plants strongly suggests that Section. The practically entire leaves separate it from most of the allied species. The apex of the leaf is frequently peculiar, being suddenly contracted just below the summit, on one side only, with an angle which amounts to a tooth, giving an abrupt asymmetrical tip to the leaf.

**FISSIDENS PACHYPHYLLUS** Dix., sp. n. (Pl. 1, fig. 10.)

§ *Pachyfissidens*.

*Caespites* extensi, densi, *olivaceo-nigri*, *rigidi*; caules 2–3 cm. alti, lignosi. *Folia* confertissima, erecta, vix patentia, frondem linearem, complanatam, *angustissimam*, vix 2 mm. latam, sistentia. *Folia* parva, 2 mm. longa, 0.3 mm. lata, e basi vaginante anguste ovali raptim in laminam angustam, crassam, lanceolato-subulatam contracta. Lamina dorsalis perangusta, infra angustissime decurrens. Fructus ignotus.

*Hab.* Submerged sandstone rocks in river, c. 800 m., Ulu Koyan, Sarawak, 22 Sept. 1932; coll. Oxford Exped. (2039).

A smaller and more slender, but more rigid and wiry, plant than *F. grandifrons*, and in the very narrow leaves more like the South African *F. fasciculatus* Hornsch., but with shorter stricter leaves than either, with the more or less ovate sheathing base narrowed abruptly to the thick rigid subula of subequal length, while in the other two species the narrowly lanceolate base tapers very gradually into the long, somewhat flexuose subula. The basal cells also are slightly larger.

It is a quite distinct species in the form of the leaves, whereas the three plants from Yunnan and Japan, described by Bescherele as new species, are scarcely separable from *F. grandifrons*.

#### CALYMPERACEAE.

**SYRRHOPODON REVOLUTUS** Doz. & Molk.

Samawang River, near Sandakan, 12 July 1927; coll. C. Boden Kloss (18692). Base of tree in white sand, under 300 m., Marudi, Sarawak, Nov. 1932; coll. Oxford Exped. (2667). Tree-trunk, near sea-level, Santubong, Sarawak, Dec. 1932; coll. Oxford Exped. (2733). A curious form with numerous short, fasciculate, apical branches, giving the stems an almost dendroid habit.

**SYRRHOPODON BORNENSIS** (Hampe) Jaeg. var. nov. **ROBUSTUS** Dix.

*Procerus*; caules usque ad 8 cm. alti; folia 2.5–2.75 mm. longa, 0.5 mm. lata; limbus folii prope basin circa 25  $\mu$  latus. Cellulae superiores aequae ac limbus plerumque chlorophyllosae.

*Hab.* On tree-trunk, c. 4 m. from ground, in open moss forest, 1,300 m. alt., Dulit Ridge, Sarawak, 8 Nov. 1932; coll. Oxford Exped. (2529); in dense bright green tufts, reddish below. On base of fern recently fallen from tree-tops, in shady moss forest, alt. c. 1,230 m., Dulit Ridge, Sarawak, 20 Sept. 1932; coll. Oxford Exped. 1932 (1999).

I find no structural differences from *S. bornensis*, but the habit and size are remarkable; the leaves are in all their dimensions about twice the normal size.

**SYRRHOPODON CONFERTUS** Lac.

Tree-trunk in primary forest, in small, round, vivid green cushions, G. Dulit, Sarawak, 23 Aug. 1932; coll. Oxford Exped. (1417). Sandstone rock ledge, c. 800 m., Dulit Ridge, Sarawak, 29 Aug. 1932; coll. Oxford Exped. (1585).



## SYRRHOPODON SUBCONFERTUS Broth.

Tree-trunk in rain-forest, c. 650 m., Dulit Trail, Sarawak, Nov. 1932; coll. Oxford Exped. (2641).

New to Borneo. *Distr.* Andaman Is., Malay Penins.; Siam.

## SYRRHOPODON ASPERRIMUS Broth.

Hayoep, South-east Borneo, 13 June 1908; coll. Hubert Winkler; Herb. Kew. (2447).

New to Borneo. *Distr.* Solomon Is.; Duke of York Is.

This differs very slightly from the original (of which I have seen only the description) in having the nerve sometimes slightly scabrous dorsally at the apex; the leaves there are described as obtuse, while here (though much less acute than in *S. rufescens*) they are shortly and bluntly pointed. It would seem at most to be a varietal form.

## SYRRHOPODON RIDLEYI Broth.

Balambanyan Is., Borneo, 11 Sept. 1927; coll. C. Boden Kloss (19281).

New to Borneo. *Distr.* Malay Penins.

## SYRRHOPODON TRISTICHUS Nees.

Shrub in forest by torrent, under 300 m., G. Dulit, Sarawak, 17 Nov. 1932; coll. Oxford Exped. (2620).

## SYRRHOPODON ALBO-VAGINATUS Schwaegr.

Dulit Trail, Sarawak, Aug. 1932; coll. Oxford Exped. (1355).

## SYRRHOPODON SUBACAULIS Dix., sp. n.

Eu-Syrrhopodon. § Acaules.

Corticola. Dense gregarius, pallide olivaceus, *fere acaulis*. Habitus *Calymperidii*. Folia *sicca madidaque stricta*, erecta; e basi brevi lanceolata, longe *linearia*, apice breviter obtuso-acutato; folia 6-7 mm., basis 1.5 mm. longa; cancellina totam partem vaginantem occupans; costa validiuscula, *carinata*, laevis, percurrent. Folia limbo hyalino cartilagineo latiusculo, *integerrimo*, *ubique, nisi summo apice, obtuse parce denticulato* circumdata, parte basilari e cellulis marginalibus pluriseriatis tenuissimis, margine minutissime denticulato, instructa. Cellulae laminae minutae, 5-6  $\mu$  latae, pellucidae, dorso sublaeves.

Cetera ignota.

*Hab.* Tree-trunk in primary forest, under 100 m., G. Dulit, Sarawak, 17 Aug. 1932; coll. Oxford Exped. (1327 b).

Clearly belonging to the small group of species hitherto known only from tropical America, marked by the narrow rigid leaves, giving the plant the appearance of a stemless *Calymperidium*, but at once distinguished by the hyaline border of the leaves.

**SYRRHOPODON ABERRANS** Broth. var. nov. **LAEVIS** Dix.

A forma typica differt foliorum apice *lato, obtuso, saepe subretuso*, apiculo reflexo, cellulis *laevibus*, costa dorso *laevi*.

*Hab.* Hollow at base of tree-trunk, c. 1,400 m., Dulit Ridge, Sarawak, 5 Oct. 1932; coll. Oxford Exped. (2140).

Very different from the typical form described by Brotherus in the above characters. But specimens of the original sent me by Brotherus showed the nerve nearly always smooth, and the upper cells mostly quite smooth; so that the difference is not so wide as would appear, and can be considered varietal only. The broad subretuse apex is very marked, but here and there a leaf is found with pointed apex, as in the type.

**SYRRHOPODON FLAMMEO-NERVIS** C. M. var. nov. **ROBUSTUS** Dix.

*Caules elati*, ad. 7 cm. alti, *robusti*.

*Hab.* Moss forest, c. 1,100 m., G. Laiun, Sungai Balapau, Ulu Tinjar, Sarawak, 2 Nov. 1932; coll. Oxford Exped. (2381), type. Wet shaded rock, on mountain, c. 850 m., Dulit Trail, Sarawak, 29 Aug. 1932; coll. Oxford Exped. (1813). Ditto, Ulu Koyan, c. 800 m., 15 Sept. 1932 (1850), a form with laxer, rigid, divaricate leaves. Mt. Manansal, Palawan, Philippines, May 1929; coll. Edano; Herb. Bur. of Sci., Manila (80869).

C. Müller described his plant as 'pusillus'; but Brotherus places it in the Section Proliferi, with elongate stems. The above plants agree with smaller Philippines specimens which I possess in everything but the much larger size.

Species new to Borneo. *Distr.* Philippines.

**SYRRHOPODON SCALARIFORMIS** Dix., sp. n.

*S. flammeo-nervi* C. M. proximus et affinis. Differt caulibus *dense foliosis*, flavescentibus; foliis e basi angustiore, minus abrupte contracta, cellulis cancellinae superne per costam *scalariformibus*, limbo marginali supra partem basilem plus minusve distincte, sparsim *denticulato*; cellulae superiores dense, spinulose, inferiores minus alte papillosae; papillis saepe bicuspidatis.

*Hab.* At base of trees and on ground in white sand-forest, c. 950 m., Ulu Koyan, Sarawak, 15 Sept. 1932; coll. Oxford Exped. (1866), type. On ground in moss forest on exposed peak, c. 1,400 m., Dulit Ridge, Sarawak, 17 Sept. 1932; coll. Oxford Exped. (1902).

Quite distinct from *S. flammeo-nervis* in the habit, the border at shoulder variously spiculose (there entire), but occasionally entire, the cancellines scalariform above (in *S. flammeo-nervis* they are scarcely so at all, but rather of the 'Euryeycla' outline); apparently also in lacking the orange colour which the leaf-base often shows when old in that species. I have given it the name *scalariformis* to indicate its distinction from that plant, without suggesting that the character is pronounced as compared with other species of the genus. It is less marked, perhaps, in no. 1902, but the dentation of the shoulder is conspicuous there. The type is only about 2 cm. high; no. 1902 is much taller, yellowish above, but brown below.

**SYRRHOPODON CILIATUS** Schwaegr.

G. Dulit, Sarawak, Aug. 1932 ; coll. Oxford Exped. (1261).

**SYRRHOPODON SPICULOSUS** Hook. & Grev.

G. Santubong, Sarawak, c. 900 m., Dec. 1932 ; coll. Oxford Exped. (2731).

**SYRRHOPODON RICHARDSII** Dix., sp. n. (Pl. 1, fig. 11.)

Eu-Syrrhopodon. § Cavifolii.

Tenellus, dense gregarius, crispifolius, habitu *S. cavifolii* seu *S. trachyphylli*, sed gracilior, et costa dorso *laevissima* longe distans. A *S. gracili* Mitt. et *S. Lilliei* Broth. foliis multo latoribus, apice recurvo, limbo multo brevior distincte alienus. Folia e basi brevi erecta parum seu haud dilatata patentia, lingulata, haud acutata, apice *recurvo, late apiculato* ; costa tenuis, dorso laevis, apice superficie ventrali saepe gemmas hyalinas numerosas breves articulatas gerens. Cancellina parva, e cellulis fere aequalibus instructa. Limbus hyalinus ad basin atque ventrem latiusculus, supra *cito angustatus*, vix supra basin attingens, ad ventrem *aut integer aut dentibus 3-4 brevibus*, armatus. Cellulae laminae majusculae, incrassatae, dorso grosse tuberculose unipapillatae ; margines parte superiore folii grosse arcte spinulose denticulati.

Fructus haud visus.

*Hab.* On tree-trunk, 3 m. above ground, in rain-forest on steep ridge, in wide carpet, c. 550 m., Dulit Trail, Sarawak, 9 Aug. 1932 ; coll. Oxford Exped. (1177, 1184).

A quite well-marked species, though nearly allied to several Pacific and Malayan ones, the differences from which are, however, clearly defined, and are indicated in the above description. *S. subelimbatus* Dix. from Siam has the border at the shoulder much more spiculose ; the short stems, less concave leaves, scarcely crisped when dry, &c., also separate it.

**SYRRHOPODON PATENS** Dix., sp. n.

Gracilis ; circa 2 cm. altus ; formas minores *S. tristichi* memorans ; folia e basi erecta sicca et madida *patentia*, laxiuscula, rigida, circa 5 mm. longa ; e basi oblonga, supra haud dilatata, longe *lingulata*, ad apicem abrupte acuta, plerumque longe spiculose cuspidata. Margines apud summam partem vaginantem *dentibus paucis spiculosis* praediti, superne integri, angustissime hyalino-limbati, ad summum apicem fortiter arcte spinosi. Costa valida, inferne laevis, superne leniter muricata, parte tertia superiore *dorso et ventri spiculis altis saepe subincurvis spinosa*. Cellulae superiores minutae, papillis *majusculis sed humilibus* obscurae ; infra sensim elongatae, pellucidiores, laeves, basin versus seriebus pluribus lineares, angustissimae, limbum latiusculum instrumentes. Cetera ignota.

*Hab.* Base of trees and ground in forest, c. 950 m., Ulu Koyan, Sarawak, 15 Sept. 1932 ; coll. Oxford Exped. (1866 c). With *S. Gardneri* and *S. scalariformis*. Resembling in habit *S. tristichus* Nees and *S. albidus* Thw. & Mitt. ;

and also *S. spiculosus* Hook. & Grev., *S. patulifolius* Thér. & Dix., &c. Differs from the former group in the margin of the leaf at the shoulder being distinctly, though sparsely spiculate, from the latter in the less pronounced toothedness of the shoulder and in the cells very lowly papillose. The spines on the face and back of the nerve in the upper part of the leaf are scarcely noticeable when the surface of the leaf is viewed; but when seen sideways, or in profile, they are very strong, equalling in height almost the thickness of the nerve and often pointing forward or incurved.

*SYRRHOPODON GARDNERI* (Hook.) Schwaegr.

At base of trees and on ground in white sand forest, c. 950 m., Ulu Koyan, Sarawak, 15 Sept. 1932; coll. Oxford Exped. (1866 b).

New to Borneo. *Distr.* North India; Ceylon; Java; Siam.

*SYRRHOPODON WALLISII* C. M.

Branch of tree, c. 70–80 ft. from ground, in primary forest, under 300 m., G. Dulit, Sarawak, 15 Aug. 1932; coll. Oxford Exped. (1288). *Ibidem*, branches of tree, c. 90–100 ft. from ground, 17 Aug. (1316).

New to Borneo. *Distr.* Malay Penins.; Great Natunas; Philippines; Celebes.

*SYRRHOPODON UNDULATUS* (Doz. & Molk.) Lindb.

Near Kabayan, Brit. N. Borneo 180 m., 27 Nov. 1931; coll. Holttum (25174).

*SYRRHOPODON FASCICULATUS* Hook. & Grev.

G. Landa, Borneo, 1912; coll. J. A. Anderson; Herb. Singapore Bot. Gard. (838).

*SYRRHOPODON MUELLEKI* (Doz. & Molk.) Bry. jav.

Trunks of small trees in rain-forest, under 300 m., G. Dulit, Sarawak, 7 Aug. 1932; coll. Oxford Exped. (1146). *Ibidem* (1146 bis), var. *strictifolius* (C. M.) Dix.

*CALYMPERES DOZANUM* Mitt.

Tree-trunks, Marudi, Baram, Sarawak, 24 July 1932; coll. Oxford Exped. (1001).

*CALYMPERES SARAWAKENSE* Dix., sp. n. (Pl. 1, fig. 12.)

Hyophilina. § *Stenocycla*.

Pusillum, fere acaule, dense gregarium, pallide viride. Folia stellatim patentia, 3–4 mm. longa, medio folio 0.5–0.6 mm. lata, e basi angustissima sensim latiora, longe spathulato-lingulata, apice late rotundato, obtusissimo, concava, marginibus valde undulatis, integris, seu cellulis prominentibus ubique arcte crenulatis. Costa validiuscula, e basi sensim angustata, sub summo apice abrupte soluta, dense grossiuscule muricata. Cellulae minute rotundatae,

chlorophyllosae, subincrassatae, dorso papilla singula magna altiuscule papillosae. Cancellina *perparva*, nunc fere nulla, nunc melius evoluta, e cellulis circa 6-8-seriatis tantum altis, versus marginem sensim angustioribus, marginalibus vix ullis, breviter rectangularibus, cancellinis supra in cellulas laminae sensim vel abrupte transeuntibus. *Teniola nulla*.

Cetera ignota.

*Hab.* Trunk of tree in primary forest, under 300 m., G. Dulit, Sarawak, soc. cum *Syrrhopodonte subacauli*, 17 Aug. 1932; coll. Oxford Exped. (1927 a).

Distinct from all the species of the group in the long, very narrow leaves, broadest about the middle, with curiously undulate margins and highly unipapillate cells. The cancellina may be reduced to a few indistinct cells, and at the most is extremely small, though extending almost the width of the remarkably narrow base.

#### CALYMPERES HAMPEI Doz. & Molk.

On dead wood in garden, Santubong, Sarawak, Dec. 1932; coll. Oxford Exped. (2732).

#### CALYMPERES TENERRIMUM Dix., sp. n.

Hyophilina. § Climacina.

Pertenellum, pallidum, caulis brevissimus, vix 0.5 cm. altus. E. speciebus Indo-malayanis *C. Vriesei* solum affine; ab eo differt statura minore, foliis angustioribus, vix 0.5 mm. latis, *minus concavis*, *teniola minus evoluta*, marginibus *multo confertius, fortius* dentatis, apice *magis sensim acutato*, cellulis *pellucidis, laevibus*. Folia abnormalia e basi brevi longe linearia, costa crassa papillosa, lamina angustissima.

Cetera ignota.

*Hab.* On rotten log in heath forest, under 300 m., Forest Reserve, Marudi, Sarawak, Nov. 1932; coll. Oxford Exped. (2674 b).

Very near to *C. Vriesei*, but apparently quite distinct in the characters italicized above.

#### CALYMPERES LATICUSPIS Dix., sp. n.

Eu-Calymperes. § Himantina.

*C. takitensi* Sull. (*C. orientale* Mitt.), etc., affine; olivaceum, circa 2 cm. altum. Folia circa 8 mm. longa, e basi erecta, *amplexicauli, obovata*, late lingulata, late *obtusio-acuta*, marginibus haud incrassatis, ad basin integris, medio folio sat distanter, prope apicem conferte spinuloso-serratis. *Teniola nulla*. Cellulae pellucidae, subincrassatae, longitudinaliter seriatæ, laeves, marginales 2-3-seriatæ *minores, minus pellucidae*. Costa valida, sub apice soluta.

Fructus ignotus.

Bark of tree in damp rocky rain-forest, under 300 m., G. Dulit, Sarawak, in dull green, slightly glossy tufts, 8 Aug. 1932; coll. Oxford Exped. (1161).

A combination of characters, the non-thickened margin, entire absence

of teniole, and broadly pointed apex distinguishes this species markedly from the allied plants. The cancellina ends above in a rounded apex, not joined to the nerve, much as in the *Eurycycla* group of the *Hyophilina* Section; this also separates it from several of the allied species, where the cancellina cells ascend in scalariform fashion towards the nerve.

*CALYMPERES ELATISSIMUM* Fleisch.

Kom Berg, W. Koetai, Borneo, Nov. 1925; coll. F. H. Endert (5384), Herb. Hort. Bot. Bog. (2515).

New to Borneo. *Distr.* Celebes.

This magnificent species has been recorded hitherto only from the original locality, coll. Teysmann. It is masked, in Brotherus, Musci, ed. ii, p. 240, under the name *C. altissimum*. A remarkable feature of it is that the leaves are frequently more strongly recurved when dry than when moist.

Fleischer in his description makes no special reference to the abnormal leaves. They are remarkable in that they are produced, not as is usual, from the upper part of the stem, but along the length of it, alternating often rather regularly with the normal leaves; and being more or less erect, rigid, bristle-shaped, with a large apical tuft of gemmae, they contrast strikingly with the broad recurved normal leaves.

*CALYMPERES BECCARII* Hampe

Tree-roots in river-bank, submerged in floods, under 300 m., G. Dulit, Sarawak, 31 Aug. 1932; coll. Oxford Exped. (1583), f. *elata*.

*CALYMPERES LONGIFOLIUM* Mitt. (*Syrrophodon calymperidioides* Broth.).

Koala-Koeroen, Borneo, 1924; coll. H. Lampmann, Herb. Herzog (22). Near Long Kapa, G. Dulit, Sarawak, 1932; coll. Oxford Exped. (s. n.), c.fr. The fruit is of very rare occurrence.

Brotherus's Borneo plant of the above name has proved to be this species.

POTTIACEAE.

*CHIONOLOMA LONGIFOLIUM* Dix., sp. n. (Pl. 1, fig. 13.)

Robustum, *elatum*, caules ad 8 cm. alti, simplices vel parce ramosi, flexuosi, laxe caespitosi. Folia sat conferta, patentia, sicca flexuosa, curvata, vix crispata, praelonga, usque ad 1 cm. longa, e basi *brevi*, paullo latiore, sensim late lingulato-lanceolata, supra latiuscule, longiuscule acuminata, ut in *C. indurato* (Mitt.), marginibus apud apicem fortiter involutis. A *C. latifolio* Dix. differt foliis multo longioribus, cellulis superioribus multo minus obscuris, *longioribus*, atque limbo folii minus distincto, e cellulis *brevioribus*, minus *cartilagineis* instructo.

Fructus ignotus.

*Hab.* Borneo, 1896-97, coll. Jaheri, Exped. Nieuwenhuis; Herb. Hort. Bot. Bog. (2563 a).

Very distinct from the two described species in the long flexuose leaves, in form and structure somewhat between the two; the longly and narrowly acuminate points are more like those of *C. induratum*, but in the cell-structure and much less marked hyaline border it resembles more closely *C. latifolium*. It differs from both also in the cell-structure. In both those species the elongate, more or less distinct cells of the slightly expanded base give place abruptly, almost at the shoulder, to the minute, very obscure, and opaque upper cells. Here the basal cells remain unaltered for a long distance up the leaf (approximately one-third), far above the basal part, and then pass rather less abruptly, in Tortelloid fashion, into the obscure cells; the hyaline border reaches some way above this point to about mid-leaf, but is much less differentiated than in *C. induratum*, being formed of quadrate or slightly elongated cells only.

The opacity and obscurity of the cells in this species appears to be due to the opaque cell-contents, which fill the entire cell, and are either in closely adjacent globules arranged in a catenulate fashion or in a single mass regularly constricted at the sides at intervals (it is not easy to say which), so as to give the cells an exactly Rhacomitrioid appearance, which is continued to the upper part of the leaf.

STEPHANODICTYON Dix., nov. genus Pottiacearum.

Habitus Trichostomoideus. Folia praelonga, linearia, aciculari-acuminata, fragilia. Costa valida, sectione transversa elliptica, duces centrales circa 7 majusculas, stereidarum cohortes latiusculos et dorsales et ventrales, seriem unicam cellularum superficie ventrali paullo majorum inanarum exhibens. Cellulae basiliares hyalinae, laminae parvae, subquadratae, vel breviter rectangulares, parietibus incrassatis, omnibus utraque superficie regulariter, catenulate, papillis seriatim coronatis.

Fructus ignotus.

STEPHANODICTYON BORNEËNSE Dix., sp. n. (Pl. 1, fig. 14.)

Robustiusculum. Laxe caespitosum, flavo-fuscescens; caules circa 1.5 cm. alti, plerumque simplices. Folia sat conferta, undique patentia, fragillima, sicca laxè flexuoso-contorta; longissima, 1 cm. vel paullo ultra, e basi subvaginante paullo latiore longe linearia, sensim longissime aciculari-acuminata, carinata, marginibus planis, integris vel rarius hic illic sparsim obtuse denticulatis, ceterum teneriter crenulatis. Costa inferne lata, circa 180  $\mu$ , sat opaca, superne sensim angustata, pellucida, apice in cuspidem pellucidam laevem saepe excurrentes. Cellulae basiliares pauci, teneri, hyalini, rectangulares vel elongate hexagonae, parietibus tenuibus, supra magis magis incrassatis, juxta costam in cellulis laminae cito transeuntes, sed ad margines oblique adscendentes, limbum hyalinum praealtum instruantes. Cellulae laminae inferne breviter rectangulares, vel ellipticae, circa 2  $\times$  1, versus apicem paullo breviores, ibique marginales seriebus pluribus subquadratae, omnes incrassatae, lumine saepe anguste elliptico, parietibus, praecipue longitudinalibus, seriatim papillis coronatis, unde cellulae faciem Rhacomitrioidem exhibent.

*Hab.* Lobang, Kinabalu, c. 1,225 m., on rock in forest, 19 Nov. 1931; coll. Holttum (25637).

Monsieur Thériot agrees with me that in spite of the absence of fruit this must be considered the type of a new genus. The extremely long acicular leaves, the Tortelloid areolation of the basal part with the hyaline border reaching far up the leaf, and the extreme fragility of the leaves are in themselves characters which would make it difficult to place the plant in any known genus, while the cell-sculpture is distinct from anything else in the family; the seriate catenulate papillae all round the cell with the appearance of a miniature coronet surrounding it suggests the generic name which I have given to the plant; superficially the cells have a somewhat Rhacomitrioid appearance, but closer examination shows that this is due to external papillae, not internal thickening of the cell-walls. The nerve is not unlike that figured by Limpricht for *Trichostomum cylindricum* (Bruch), but wider and less thickened.

LEPTODONTIUM KINABALUENSE Dix., sp. n. (Pl. 1, fig. 15.)

E minoribus generis. Dense caespitosum, stramineum, inferne atrofusum. Caulis vix 2 cm. altus, parce ramosus. Folia conferta, *difficillime emollita*, *erecto-patentia*, circa 2.5 mm. longa, e basi vaginante erecta, late ovato-lanceolata, peracuta, versus apicem *argute*, *irregulariter*, *fortiter* dentata, marginibus basilaribus aut planis aut ad medium folium revolutis. Costa valida, sub summo apice soluta, dorso superne muriculata. Cellulae subquadratae, incrassatae, longitudinaliter seriatæ, circa 11  $\mu$  latae, ubique super lumen atque parietes dense humiliter papillosae, unde paullo obscurae, seriebus marginalibus nonnullae minus papillosae, inde paullo minus obscurae; inferne sensim majores, elongatae, basilares rectangulares, hyalinae.

Fructus haud visus.

*Hab.* Kinabalu, 4,080 m., 14 Nov. 1931; coll. Holttum (25685), typo. Ibidem (25688).

The genus is new to Borneo. *L. humillimum* Broth., from Lombok, is near our species, but has much smaller leaves, less acutely pointed, less strongly toothed; and the cells are described as 'dense verrucosis', while here they are very lowly papillose, so as hardly to show in profile, but being scattered over both the cell lumen and the walls they render the areolation obscure; this is less marked on several marginal rows, which therefore show a very faintly marked border, scarcely visible at all in some leaves.

*L. dentatum* Wils., like *L. flexifolium* Hampe, has narrower, more regularly and strongly toothed leaves. The Javan *L. Warnstorffii* Fleisch. is very near it, but has much smaller leaves, less sharply toothed, with smaller, much more obscure cells.

HYOPHILA MICHOLITZII Broth.

Stream below Dallas, 800-900 m., Brit. N. Borneo, 9 Nov. 1931; coll. Holttum (25372 p.p., 25373).

New to Borneo. *Distr.* Wide.



I very much doubt whether *H. Micholitzii* Broth. and *H. Dozy-Molkenboerii* Fleisch. be distinct species. Fleischer gives some very slight and rather elusive distinguishing characters, principally in that the leaves in the former are comose, and the inner perichaetial leaves crenulate, while in the latter the stems are equally foliate and the bracts entire. In the present plant the inner perichaetial bracts are distinctly crenulate, but the leaves are not comose. I think Fleischer's name should be dropped.

*BARBULA INDICA* (Schwaegr.) Brid.

Moist limestone rocks at mouth of cave, under 300 m., Bidi, Sarawak, Dec. 1932; coll. Oxford Exped. (2750). A tall robust form, 6 cm. high, sterile.

*BARBULA OBSCURIRETIS* Dix.

Muddy banks by river, R. Tinjar, Sarawak, under 300 m., 20 Aug. 1932; coll. Oxford Exped. (1376).

New to Borneo. *Distr.* Siam; Philippines.

#### GRIMMIACEAE.

*RHACOMITRIUM LANUGINOSUM* (Hedw.) Brid.

Kinabalu, c. 2,600 m., 14 Nov. 1931; coll. Holttum (25669). *Ibidem*, c. 2,750 m., 14 Nov. 1931 (25697).

This is not mentioned in Dr. Stapf's or Miss Gibbs's lists, and is probably new to Borneo.

#### ORTHOTRICHACEAE.

*DESMOTHECA APICULATA* (Doz. & Molk.) Lindb.

Long Pochoes, W. Koetai, Borneo, Aug. 1925; coll. F. H. Endert (2461), *Herb. Hort. Bot. Bog.* (2538).

*MACROMITRIUM MINUTUM* Mitt.

Tenompok, Brit. N. Borneo, 1,400 m., 11 Nov. 1931; coll. Holttum (25692 *b*). Kian, Brit. N. Borneo, 915 m., 21 Nov. 1931; coll. Holttum (25695 p.p.).

New to Borneo. *Distr.* Ceylon; Java; Malay Penins.

Apparently the first species of the subgenus *Cometium* to be recorded from Borneo.

*MACROMITRIUM GONIORRHYNCHUM* (Doz. & Molk.) Mitt.

Kian, Brit. N. Borneo, 915 m., 21 Nov. 1931; coll. Holttum (25695).

New to Borneo. *Distr.* Wide, from Khasia to New Guinea.

*MACROMITRIUM ZOLLINGERI* Mitt.

Maraiparai, Brit. N. Borneo, 1525 m., 24 Nov. 1931; coll. Holttum (25184).

New to Borneo. *Distr.* Java; Lombok; Malay Penins.; Annam.

Brotherus places this in a Section with the cells 'fein papillös', but they are mammillose, not papillose, here, as also Fleischer describes them.

**MACROMITRIUM PAPILLISETUM** Dix., sp. n.Eu-Macromitrium. § *Leiostoma*.

*M. Blumei*, *M. Zollingeri*, etc., subsimile et forsan affine, sed valde distans. Dense confertum, humile, subrobustum. Rami *breves, turgidi, obtusi*; folia sicca arcte spiraliter contorta, quam in illis speciebus *multo obtusiora*, apice late rotundato, *brevissime apiculato*. Cellulae superiores parvae, obscurae, *opacae*, in folii dimidia parte inferiore pellucidae, elongatae, *ellipticae, grossiuscule papillosae, infimae solum perpaucae perangustae*, lineares, laeves. Folia perichaetialia acuta, longius cuspidata. Seta *perbrevis*, circa 3 mm. longa, *crassa, dense, grosse papillosa*. Theca pachydermica, *brevis, late urceolata, macrostoma*, operculo e basi *subplana* brevirostrato; calyptra dense, breviuscule pilosa. Peristomium nullum.

*Hab.* Bettotan, Sandakan, 23 July 1927; coll. C. Boden Kloss (18742).

A striking species in the short, stout, highly papillose seta and the short, wide, urceolate capsule. *M. Winkleri* Broth., from Borneo, has quite different leaves, longer, strongly tubercular cells, smooth seta, &c.

**MACROMITRIUM LONGICAULE** C. M.

Brit. N. Borneo, Nov. 1931; coll. Holttum; in stream below Dallas, 760 m. (25371); Tenompok, 1,340 m. (25692, 25693).

New to Borneo. *Distr.* Java; Philippines.

An interesting extension of the range of this rare and fine species.

**MACROMITRIUM OCHRACEUM** (Doz. & Molk.) C. M.

G. Rumpit, Aug. 1912; coll. J. W. Anderson, Herb. Singapore Bot. Gard. (185). Koobambang River, 1,200 m., Kinabalu, 8 Aug. 1933; coll. J. & M. S. Clemens (34368). Maraiparai Ridge, Kinabalu, 1,520 m., 24 Nov. 1931; coll. Holttum (25623). Moss forest, Dulit Ridge, 1,200–1,400 m., Sarawak, 1932; coll. Oxford Exped. (1,100 b). On branches of fallen tree in shady moss forest, c. 1,250 m., Dulit Ridge, Sarawak, 13 Sept. 1932; coll. Oxford Exped. (1877). A slender form, with the leaves much shorter, strongly, regularly, and prettily recurved when moist. Dulit Ridge, c. 1,300 m., Sept. 1932; coll. Oxford Exped. (1880, 1905). A very striking form, with close, regular, subequal pinnate branching.

This beautiful species appears to be abundant in some of the mountainous parts of Borneo, but has not been hitherto recorded. I cannot see, from the description, how *M. rubricuspis* Broth. differs.

**MACROMITRIUM OCHRACEOIDES** Dix., sp. n. (Pl. 2, fig. 17.)

*M. ochraceo* colore, seta papillosa, calyptra valde pilosa, atque fructu simile et affine; differt habitu densiore, ramis confertioribus, brevioribus, foliis *brevioribus*, inferne multo *angustioribus*, 0.5 mm. (nec 10 mm.) latis, cellulis basilaribus *angustissimis*, perincrassatis, altius adscendentibus, *laevibus*; cellulae superiores plerumque isodiametricae; costa *in pilum sat longum*

*rubrum vel hyalinum* laeve, excedens. Fructus ut in *M. ochraceo*, sed theca paullo longior, angustior, ore distincte angulato. Seta 10–12 mm.

*Hab.* Between Kamborangah and Pakka, Kinabalu, 2,200–3,100 m., 13 Nov. 1931; coll. Holttum (25481), type. Ibidem, below Pakka, c. 3,100 m., 15 Nov. 1931 (25663).

The nerve in *M. ochraceum* is very shortly excurrent in a reddish cuspidate point; here it is longly piliferous, flexuose, and hyaline above, and by this the species may be recognized with the lens; it is also smaller and denser; while the more numerous smooth basal cells give another distinctive character. The supra-basal cells here are coarsely, but rather lowly tuberculate; in *M. ochraceum* they are very strongly and highly so, some cells almost to the insertion of the leaf. The angulate mouth of the capsule is another character of some importance.

**MACROMITRIUM PERDENSIFOLIUM** Dix., sp. n. (Pl. 2, fig. 18.)

E robustissimis generis, habitu *M. longipilo* et *M. cuspidato* simile. Ab hoc seta multo longiore, usque fere 3 cm. longa et ultra, *tenui*, foliis apice *multo obtusiore*, cellulis basilaribus parvis, angustissimis, breviusculis, papilla unica *tenera* sparsim coronatis. A *M. longipilo* differt seta longiore, laevi, theca ore *angulato*, apice folii *subobtusio*, cellulis basilaribus multo tenerius papillois. Fuscum. Rami 2 cm. longi vel ultra, *perdensifolii*, *turgidi*. Folia 4–5 mm. longa, e basi lata, magna breviter lingulato-lanceolata, apice lato, raptim breviter acutato vel subobtusio, costa excedente *breviter pilifero*. Theca elliptica, microstoma, laevis vel leniter plicata, ore indistincte angulato. Calyptra nuda vel subnuda.

*Hab.* Kemoel, W. Kootai, c. 1,700 m., Oct. 1925; coll. F. H. Endert (4535), Herb. Hort. Bot. Bog. (2522), type. On branch of small tree, white sand forest, c. 900 m., Ulu Koyan, Sarawak, 15 Sept. 1932; coll. Oxford Exped. (1875).

In the robust habit, long, densely foliate branches, long subpiliferous leaves, it resembles the two species with which I have compared it, but differs at once in the long thin seta, the more or less abruptly piliferous leaves, and the exceedingly narrow, dense, 'conflated' basal cells, which are finely and sparsely tuberculate. My *M. turgidum* from Siam is closely allied, but is of shorter denser habit, the leaves sharply denticulate at the apex, the excurrent nerve only shortly cuspidate, and the seta much shorter.

**SCHLOTHELMIA RUBIGINOSA** C. H. Wright

Pakka, 3,100 m., Kinabalu, 15 Nov. 1931; coll. Holttum (25643).

This very fine endemic species appears to be confined to a small area on the upper ridges of Kinabalu. C. H. Wright's comparison of the remarkable plica of the leaf to the dorsal fin of a fish is very apt. He does not mention the fact that the basal cells are tuberculate.

Brotherus in the 'Musci' has erred seriously as to this species; the calyptra is not 'longhaarig', but smooth.

*SCHLOTHEIMIA WALLISII* C. M. (*S. splendida* Mitt.).

Below Pakka, 3,100 m., Kinabalu, 15 Nov. 1931; coll. Holttum (25671). Maraiparai Ridge, 1,525 m., 22 Nov. 1931; coll. Holttum (25175); the original station for *S. splendida*, coll. Haviland.

Another very fine species, hitherto considered to be confined to the Philippines and Borneo, but I have it in my herbarium from three localities in Celebes.

The Borneo *S. splendida* is certainly identical with *S. Wallisii* C. M. The principal difference is said to be in the calyptra, in *S. Wallisii* 'dentibus asperis robustis scabra', while in *S. splendida* it is 'pilis brevibus adpressis adpersa', which does not seem to indicate a wide difference! Brotherus attributes to *S. Wallisii* a calyptra 'mit groben Zähnen besetzt', but in specimens from Luzon I find the calyptra very minutely hispid. That the hairiness of the calyptra varies considerably is evident from the fact that Holttum's plants have them quite smooth (on one I saw a single hair!). And in the specimen of *S. Wallisii* at Kew the single calyptra present is almost or quite naked.

The leaves in this species show a great variability, being sometimes distinctly spirally twisted when dry, sometimes not at all. Mitten's plant has the leaves described as 'laevia', while in *S. Wallisii* they are 'rugulosa'; in Holttum's specimens they are decidedly rugulose, though in this too they vary much.

## LEPTODONTIOPSIS Broth.

I follow Hilpert ('Studien zur Systematik der Trichostomaceen') in placing this genus in Orthotrichaceae.

## LEPTODONTIOPSIS ORIENTALIS Dix., sp. n. (Pl. 2, fig. 16.)

Caespitosa; superne flavescens, infra *aurantiaca*; caules *robusti*, haud elati, usque 2.5 cm. alti, inferne dense tomentosi. Folia dense conferta, *recurvo-squarrosa*, haud fragilia, sicca *flexuosa*, *undulata*, ubique patentia, *praelonga*, usque ad 4 mm. longa, 0.5 mm. lata, e basi brevissima vaginante angusta *longe lingulata*, e medio folio fere sensim longissime acuminata, apice *longe, flexuose cuspidato vel breviter pilifero*. Margines plani, ubique fore minute, ad apicem fortiter crenulati, rarius distincte denticulati. Costa sat valida, carinata, infra apicem soluta. Cellulae rotundatae, vel ellipticae, valde incrassatae, alte dense papillosae, basillares raptim elongatae, *lineares, hyalinae vel aurantiacae*, parietibus tenuibus.

Perichaetii folia vix distincta. Seta circa 1.5 cm. alta, tenuis, leniter *flexuosa*, vetustate fusca. Theca elliptica vel fusiformis, deoperculata, 2 mm. longa, *microstoma*, *gymnostoma*, sicca ore paullo angulato; cetero laevis, fusca; operculum oblique tenuirostratum; calyptra longa, angusta.

*Hab.* On rotten wood, 3,500 m., Kinabalu, 14 Nov. 1931; coll. Holttum (25668), type. Ibidem (25689). The latter a smaller, denser, sterile form.

A remarkable extension of the range of this well-marked genus, hitherto known only from two tropical African species. The leaves in the present

plant are very similar to those of *L. elata* Dix., but are more finely acuminate, with the basal cells more clearly differentiated, hyaline, with thin walls. The habit is quite distinct. The older leaves are orange-red, and the basal hyaline part is frequently variegated with orange rows of coloured cells descending to the base, and alternating with strips of the hyaline ones. The entirely gymnostomous fruit appears very similar to that of the African *L. fragilifolia* Broth.

The leaves have a remarkable similarity in form, structure, and colour to those of *Macromitrium ochraceoides* Dix. !

### SPLACHNACEAE.

TAYLORIA BORNEËNSIS Dix., sp. n. (Pl. 2, fig. 20.)

Orthodon.

Stirps pulcherrima, magna; inter alios muscos crescens. Caulis circa 2 cm. longus, robustus; folia magna, circa 4 mm. longa, 1-1.25 mm. lata, e basi angustiore brevi, late oblonga, late spathulata, subobtusa, marginibus planis, parte superiore *distanter, grosse, argute dentata*. Costa tenuis, ad folii basin atque saepe ad basin acuminis dilatata, apice in cuspidem robustum laevem longem excurrans. Areolatio laxa, e cellulis elongate hexagonis, parietibus firmis, 20-27  $\mu$  latis, instructa, versus margines haud mutata; cellulae inferiores latiores, late rectangulares, perpellucidae.

Seta *praelonga*, 3-4 cm. vel paullo ultra, crassiuscula, rubra; theca erecta, circa 4 mm. longa, e collo defluente angustiore elliptico-cylindrica, fuscescens; operculum magnum, pallidum, alte hemisphaericum, apiculatum. Calyptra magna, 6-8 mm. longa (cum pilis), *anguste conica, pulchre vinoso-rubra*, basi laciniata, pilis longis sericeis flavis dejectis oblecta.

*Hab.* Tenompok, Brit. N. Borneo, 1,440 m., 11 Nov. 1931; coll. Holttum (25329).

A fine species, allied to *T. indica* Mitt. and *T. imbricata* Thw. & Mitt., differing from the former in the shorter, broader, more obtuse leaves, from the latter in the much larger size of all its parts and the non-concave leaves; from both in the longer seta and beautifully vinous red conspicuous calyptra.

### FUNARIACEAE.

FUNARIA BORNEËNSIS Dix., sp. n. (Pl. 2, fig. 19.)

Entosthodon.

*F. Buseanae* (Bry. jav.) forsan affinis. Seta robusta. Caulis circa 5 mm. alta vel ultra, simplex, inferne subnuda, apice rosulatus. Folia majuscula, inferiora orbiculato-ovata, superiores e basi paullo angustiore spathulato-ovata, *breviter late acutata*, marginibus *integris vel subintegris*, costa longe sub apice soluta, vel nonnunquam subpercurrans; cellulae majusculae, late elongate hexagonae vel hexagono-rectangulares, marginales serie unica *multo angustiores*, limbum colore saturato sat distinctum instruantes.

Seta circa 1 cm. alta, crassiuscula. Theca e collo *longo* defluente subpyriformis, suburceolata, *leniter asymmetrica et gibbosa*, macrostoma; ut videtur gymnostoma.

*Hab.* Pakka, 3,100 m., 15 Nov. 1931 ; coll. Holttum (H).

The fruit is not in good condition, being either immature or over-ripe ; it is therefore not quite clear what is the affinity of the plant. The capsule, however, is probably gymnostomous, or the peristome imperfect or fugitive, and is certainly asymmetric and gibbous. The habit of the plant, with the leaves almost confined to a rosulate tuft at the top of the stem, the shortly pointed, entire (or practically entire) leaves, with a distinct row of narrow, often deeply coloured, but otherwise undifferentiated cells, are distinct characters.

Apart from *F. hygrometrica* the genus has not, I believe, been recorded from Borneo.

#### MNIACEAE.

*MNIUM SUCCULENTUM* Mitt.

Below Dallas, 900 m., Brit. N. Borneo, 6 Nov. 1931 ; coll. Holttum (25278).

New to Borneo. *Distr.* North and South India ; Ceylon ; Malay Penins. ; Assam.

The leaf-margin here is sometimes subentire ; I find the same thing in specimens from Madura, South India.

#### DREPANOPHYLLACEAE.

*MNIOMALIA SEMILIMBATA* (Mitt.) C. M.

Forest Reserve, Marudi, under 300 m., on rotten log, Sarawak, Nov. 1932 ; coll. Oxford Exped. (2674).

#### RHIZOGONIACEAE.

*RHIZOGONIUM NOVAE-HOLLANDIAE* Brid.

Ridge forest, Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931 ; coll. Holttum (25655). A form with rather broader, more acuminate leaves, less toothed than usual, but showing a tendency towards the more typical form, in both outline and toothing.

New to Borneo. *Distr.* Australasia ; Patagonia ; Sumatra ; Malay Penins.

*RHIZOGONIUM SPINIFORME* (Hedw.) Br.

From numerous localities.

*RHIZOGONIUM LONGIFLORUM* Mitt. (*R. badakense* Fleisch.).

Rotten log in heath forest, Marudi, Baram, Sarawak, 25 July 1932 ; coll. Oxford Exped. (1020). Shaded rocks on mountain side, c. 850 m.,\* Dulit Trail, Sarawak, 29 Aug. 1932 ; coll. Oxford Exped. (1586).

*R. badakense* Fleisch. is certainly this species ; if the descriptions of the two species are compared it will be seen that the authors give exactly the same characters to distinguish them from *R. spiniforme*. Brotherus, it is true, puts *R. longiflorum* in a section with leaves narrowed at the base, *R. badakense* with leaves not narrowed ; but I find no appreciable or constant difference. In the Sarawak no. 1586, the leaves are in no way narrower at the base.

## BARTRAMIACEAE.

*BARTRAMIA AURESCENS* Dix., sp. n. (Pl. 2, fig. 21.)

§ *Vaginella* ?

Subrobusta ; *aureo-viridis, nitidula*. Caules stricti, 1–2 cm. alti, densifolii ; folia *densissima, sicca erecta, saepe appressa, stricta, vel apice rigide leniter curvato*, 4–5 mm. longa, e basi *oblonga*, superne haud dilatata, potius paullo angustiore, *pallida*, in laminam anguste lanceolatam, planam, sensim *valide subulatam*, strictam, subsensim angustata. Costa ad basin latiuscula, in lamina *dilatata*, male delimitata, in subulam validam, denticulatam, opacam strictam longe excurrens. Margines ubique plani, arcte denticulati. Cellulae basilares *anguste lineares, elongatae, inanes, hyalinae*, superne in cellulas laminae sensim transeuntes. Eae parvae, angustae, lineares, *valde obscurae*, apice prominente papillosae, marginales serie unica *paullo latiores, subpellucidae*.

Dioica videtur. Fructus vetustus unicus visus. Seta brevis, minusquam 1 cm. longa. Theca majuscula, *erecta, symmetrica, subleptodermica, haud vel vix plicata, microstoma* ; *gymnostoma* videtur.

*Hab.* Exposed granite rock mass near summit of Kinabalu, c. 3,650 m., Nov. 1931 ; coll. Holttum (E), type. Ibidem, 14 Nov. (B). Among *Agrostis*, Upper Kinabalu, c. 3,960 m., 1932 ; coll. J. & M. S. Clemens, Herb. Hort. Bot. Bog. (2949), Pakka Cave to Low's Peak, Kinabalu, 13 Nov. 1915 ; coll. M. S. Clemens (10674), Herb. U.S.A. Nat. Mus.

Somewhat difficult to place in the genus. The strict appressed leaves suggest *Strictidium*, but the well-defined hyaline base, though not abruptly dilated, makes it fairly certain that it belongs to *Vaginella*. The single capsule is much destroyed, and it is uncertain whether it is furrowed when dry. It is in any case erect and symmetric, somewhat thin-walled, small-mouthed, and probably *gymnostomous*.

The genus is new to Borneo.

*PHILONOTIS CALOMIORA* Broth.

Between Koung and Dallas, 400–900 m., Brit. N. Borneo, 4 Nov. 1931 ; coll. Holttum (25137).

This has already been recorded from Borneo, though Brotherus does not include it in his distribution.

★  
*PHILONOTIS LAXISSIMA* (C. M.) Bry. jav.

From the same locality as the preceding, and growing with it (25137 *bis*).

*BREUTELIA KINABALUENSIS* Dix., sp. n.

E *robustissimis* generis ; caules usque ad 10 cm. alti, ad 1 cm. lati, fusco-aurei, parce divisi. Folia *densissime* conferta, horride patentia, raro deflexa, 7–8 mm. longa, e basi *brevissima*, parum distincta, *profunde brevissime* pluri-

plicata, aurantiaca, supra dilatata, in laminam late lanceolatam, sensim latiuscule acuminata, summo apice abrupte tenui-cuspidata, leniter, indistincte pluri-plicata, marginibus planis, tenuiter denticulatis. Costa tenuiuscula, in cuspidem breviusculum subflexuosum, ad basin argute denticulatum excurrens. Cellulae sat pellucidae, parvae, lineares, parietibus incrassatis, valde porosae, apicibus sparsim spiculis; basillares subsimiles, longiores, aurantiacae, alares seriebus 2-3 magnae, hyalinae, ad marginem basilarem brevissime adscendentes.

Cetera ignota.

*Hab.* Kinabalu, c. 2,750 m., 16 Nov. 1931; coll. Holttum (25337).

One of the most robust species of the genus, in size and habit resembling only the African *B. Stuhlmannii* Broth. and *B. auro-nitens* Negri. In these species the leaves taper to a very long, flexuose subula, and are deeply plicate; in the present plant the lamina is broadly and shortly pointed, in an unusual manner for the genus, then abruptly narrowed to a short, more or less flexuose, cuspidate point; the leaves also are very lightly and inconspicuously pluriplicate, except at the base along the line of insertion, where they are deeply but very shortly plicate.

*B. longicapsularis* Dix., from New Guinea, is also closely allied, especially in the highly incrassate, porose cells, but it has a very markedly differentiated base and much narrower, finely acuminate leaves.

## HYPNODENDRACEAE.

HYPNODENDRON ARBORESCENS (Mitt.) Lindb.

Sibu, Sarawak, coll. Everett, herb. Mitten.

HYPNODENDRON BECCARII (Hampe) Jaeg.

Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931; coll. Holttum (25682, 25796). Tenompok, Brit. N. Borneo, 1,440 m., 11 Nov. 1931; coll. Holttum (25335, 25347). Lumu-Lumu, Kinabalu, 1,525 m., 18 June 1925; coll. C. H. Enriquez, Herb. Singapore Bot. Gard. (18145). Kemoel, W. Koetai, Oct. 1925; coll. F. H. Endert (4296), Herb. Hort. Bot. Bog. (2536 a). Colom-bon basin, Minatahan spur, on twigs, 1,525 m., Kinabalu, 13 Aug. 1933; coll. J. & M. S. Clemens (34440). Tree in shaded forest, c. 1,200 m., Dulit Ridge, Sarawak, 13 Sept. 1932; coll. Oxford Exped. (1785).

This appears to be a frequent moss in some parts, at least, of Borneo, where it is perhaps endemic; but it is a little-known species. It has probably in the sterile state been confused with *H. Reinwardtii* and *H. arborescens*. The former has been recorded from Borneo, but I have not seen the true plant from there. It appears to be constantly of a rich orange-colour, and that and the larger size will separate it from *H. arborescens* at least, while the smooth capsule, when present, will distinguish it at once from the allied species. Fleischer does not refer to it. Brotherus had seen no specimen. The seta is considerably shorter than in *H. Reinwardtii*, and the capsule robust and estriate—only in



the dry state, and when gathered before maturity, showing slight plication. I have sterile plants from the Philippines which probably belong to this species.

**HYPNODENDRON COPELANDII** Broth.

Kemoel, W. Koetai, Borneo, 1,600–1,700 m., Oct. 1925; coll. F. H. Endert (4542), Herb. Hort. Bot. Bog. (2582 b).

Var. nov. **LATIFOLIUM** Dix. Folia *littora*; costa *percurrentes vel breviter excurrentes*.

Near Lumu-Lumu, Kinabalu, 1,525 m., 18 June 1925; coll. C. M. Enriquez, Herb. Singapore Bot. Gard. (18146).

A quite marked variety. In the type the leaves are given as 1.5 mm. long, 0.66 mm. wide; here when 1.5 mm. long they are 1.1 mm. wide, and when 1.8 mm. long are 1.25 mm. wide. Also the type is described and figured with the nerve ceasing a little below the point; here it is usually quite percurrent in the lateral leaves, and excurrent in a short cuspidate point in the ventral (it should be noted that the row of smaller leaves is ventral, not dorsal as stated by Brotherus).

Species new to Borneo. *Distr.* Philippines; Java.

In the Kemoel plant the stems are densely tomentose, but this is probably due to the plant being closely intermixed with *Mniodendron*.

Fleischer does not give this species for Java in the Musci . . . von Buitenzorg; but it exists in the Herbarium there, unnamed; collected at Nirmala, in Dec. 1913, by C. A. Backer (2080). It is in fruit, on one stem a single seta, on another four together; 5 cm. or more in height; the capsule (deoperculate) 6 mm. and almost smooth.

**MNIODENDRON.**

(Generally cited as *Mniodendron* Lindb. But Lindberg apparently gave no diagnosis of either this or *Hypnodendron*, and it seems uncertain who is the real author of the generic names.)

The species of this genus, especially of the *divaricatum* group, are very perplexing, and I do not claim to understand them. Fleischer has suggested, in correspondence, certain distinguishing characters which appear to me as very elusive, and I doubt the value of several species; but I do not feel in a position to question them. I have endeavoured to set these differences out in the form of a Key, roughly on the lines of Fleischer's letters. It will serve as a basis for further study.

Brotherus simplifies the problem enormously by dividing the species into two groups, one with the branch-leaves having the margin unistratose, the other (including *M. Mittenii*, *M. arstinerve*, and *M. microloma*) in which it is bi-stratose. I have never yet, however, seen a specimen, at any rate of this group, with bi-stratose margin, and this classification is therefore much too good to be true!

- |    |   |                     |
|----|---|---------------------|
| 1. | { Leaves longly aristate with excurrent nerve ; robust plant . . . . .                        | <i>aristinerve.</i> |
|    | { Leaves more shortly acuminate . . . . .   | 2.                  |
| 2. | { Leaves short with wide short points . . . . .   | <i>brevifolium.</i> |
|    | { Leaves longer, with narrow acumen . . . . .   | 3.                  |
| 3. | { Marginal cells of leaves short, small, and forming a more or less distinct border . . . . . | 4.                  |
|    | { Marginal cells hardly differentiated . . . . .  | 5.                  |
| 4. | { Leaf-base narrower, ovate-lanceolate . . . . .  | <i>microloma.</i>   |
|    | { Leaf-base wider, somewhat cordate, nerve thinner . . . . .                                  | <i>Mittenii.</i>    |
| 5. | { Robust plant . . . . .  | <i>divaricatum.</i> |
|    | { Small plant . . . . .   | <i>humile.</i>      |

Fleischer also separates *M. longinerve* Broth. MS. from *M. microloma* on slight characters, but in my opinion insufficient ones, and I have not retained it.

As to *M. Mittenii* Salm. (*M. microloma* Mitt. in Trans. Linn. Soc., Bot. iv, 259 (1894), nec *M. microloma* Mitt. e Geh. in Fl. 1886), Fleischer writes that no type-specimen of Salmon's seems to exist, and he therefore bases his idea of the species on a specimen (Borneo, monte Kenepsa, 1896 ; leg. Hallier, det. E. Salmon, in Herb. Hort. Bot. Bog.). But Salmon did not suggest that his '*M. Mittenii* Salm. MS.' was a new species, he only pointed out that the name *microloma* was already in use, and he therefore suggested the name *M. Mittenii* for *M. microloma* Mitt (Borneo). The type of *M. Mittenii* Salm. is therefore the type of *M. microloma* Mitt., i.e. Burbidge's plant at Kew.

Further, I may say that I can see no distinctions except in size between *M. humile* Lindb. and *M. divaricatum* ; and I have in a single gathering from Celebes dwarf plants as figured in the Bry. jav., but passing into specimens quite indistinguishable from Javan forms of *M. divaricatum* ; while another very small plant I have from Celebes has the border of small cells of *M. microloma*, and is, I think, a form of that species.

Finally, it does not appear to me at all clear whether or not Mitten considered his Bornean plant, coll. Burbidge, identical with the plant from the Sulu Archipelago, to which he had given the same name, under which it had been published (by Goehb), or whether he had forgotten that name and intended this for a new species. Nor is it quite clear in Fleischer's letters what he intends by '*M. microloma* Mitt.' Did he mean the original Sulu Archipelago plant, or the Borneo plant ? It will be seen that the whole question bristles with difficulties !

**MNIODENDRON DIVARICATUM** (Hornsch. & Reinw.) Lindb. (*M. humile* Lindb.).

Rotten log in moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 5 Oct. 1932 ; coll. Oxford Exped. (2144).

**MNIODENDRON ARISTINERVE** Mitt.

Near Pakka, 3,100 m., Kinabalu, 15 Nov. 1931 ; coll. Holttum (25645).

MNIODENDRON MITTENII Salm. (*M. microloma* Mitt., 1894).

Lumu-Lumu, Kinabalu, 1,600 m., 18 June 1925; coll. C. M. Enriquez, Herb. Singapore Bot. Gard. (18130 *a*). On ground in moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 9 Sept. 1932; coll. Oxford Exped. (1727). Kemoel, W. Koetai, Oct. 1925; coll. F. H. Endert (3758, 4296, 2592), Herb. Hort. Bot. Bog. (2524, 2563 *b*, 2582 *a*).

MNIODENDRON KORTHALSII Bry. jav.

Penresin Hills, Sarawak, July 1892; coll. A. H. Everett (676). Sandstone boulder in slight shade in torrent, under 300 m., Dulit Trail, Sarawak, 3 Aug. 1932; coll. Oxford Exped. (1116), a dwarf form. Ibidem, on large boulder in spray of stream, c. 1,230 m., 1 Aug. 1932 (1073).

#### HEDWIGIACEAE.

RHACOCARPUS ALPINUS (C. H. Wright) Par.

Maraiparai, Brit. N. Borneo, 1,525 m., 23 Nov. 1931; coll. Holttum (25182).

#### PRIONODONTACEAE.

NEOLINDBERGIA RUGOSA (Mont.) Fleisch.

Bettotan, near Sandakan, 23 July 1927; coll. C. Boden Kloss (18741). In fairly good fruit.

New to Borneo. *Distr.* Celebes; Philippines.

I follow Brotherus in placing this genus in Prionodontaceae, as the peristome seems to be nearest to that of this family.

NEOLINDBERGIA ROBUSTA Dix., sp. n. (Pl. 2, fig. 22.)

Omnium specierum generis multo *robustissima*, tapete grossum densum sordide viride circa arboris basin formans. Caules primarii repentes, intertexti, secundarii *erecti*, parce ramosi, 4–5 cm. alti, *rigidi*, robusti, *foliis horride patentibus turgidi, obtusi, duri*. Folia conferta, *subsecunda, divaricata*, sicca vix mutata, undulata, *magna*, 3–5 mm. longa, inferne 1.5 mm. lata; e basi late cordato-ovata, infra leniter pluriplicata, cito angustata, breviter oblongo-lanceolata, haud rugosa, *perconcava, subcucullata, apice acuto subrecurvo, argute inaequaliter denticulato*; margines plani, supra medium folium minute denticulati. Costa tenuiuscula, concolor, infra apicem soluta. Cellulae superiores minutae, subisodiametricae, irregulares, *incrassatae*, laeves, marginales pluribus seriebus paullo elongatae atque pellucidiores, magis *incrassatae*; infimae juxtacostales lineares, angustissimae, versus margines breviores.

Fructus ramis lateralis; perichaetia longiuscula, bracteis externis e basi late vaginante *raptim horride stricte* cuspidatis; internis erectis, convolutis, abrupte in cuspidem *validum loriformem* strictum suberectum vel patulum, integerrimum constrictis. Seta circa 1 cm. alta, crassiuscula, infra sublaevis, superne *dense fortiter papillosa*, apice dilatato; theca elliptica, deoperculata 2–2.5 mm. longa, castanea, laevis; cellulae exothecii parvae, subisodiametricae,

irregulares ; operculum longe aciculari-rostratum ; calyptra conico-cucullata, *pubescens, vel pilis erectis appressis oblecta*. Peristomium vetustum imperfectum solum visum ; simplex videtur ; dentes aurantiaci infra orificium enati, plus minusve cohaerentes, tenues, valde irregulares, nec striolati nec papilloso, vel apice sparsim, grossiuscule papilloso ; distanter, teneriter lamellati, breves. Spori 25–30  $\mu$ .

*Hab.* On buttress of tree in rain-forest, 900–1,000 m., G. Laiun, Tinjar, Sarawak, 2 Nov. 1932 ; coll. Oxford Exped. (2370).

A magnificent species, far larger than any of the half-dozen species known of this small and peculiar genus ; forming deep, coarse, harsh masses with stiff stems and leaves. The size and form of the leaves, with widely pointed, irregularly toothed, reflexed apex, above the cucullate summit of the lamina, at once distinguishes it, apart from size and habit.

Beyond a single operculate capsule only very immature ones with calyptra, and old, partially destroyed ones were seen, and it has not been possible to ascertain clearly the structure of the peristome. It appears to be single, but it is not quite clear whether the outer peristome or the endostome is present, and it is possible that one or the other is lost.

The genus consists of six Indo-Malayan species and a single one from Hawaii.

#### SPIRIDENTACEAE.

##### SPIRIDENS REINWARDTII Nees

Kamborangah, 2,200 m., Brit. N. Borneo, 17 Nov. 1931 ; coll. Holttum (25539).

New to Borneo. *Distr.* Wide. It is remarkable that this magnificent moss should have escaped detection in Borneo until now.

#### PTEROBRYACEAE.

##### TRACHYLOMA INDICUM Mitt.

Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931 ; coll. Holttum (25682 p.p.) ; and near Pakka, 3,100 m., Kinabalu, 15 Nov. 1931 ; coll. Holttum (25647).

A rather curious form ; the branches are mostly markedly cuspidate at the tips, though on one stem they are not so at all. In the former the cuspidate tips are crowded with brood-filaments, which are also found, but in a different position, in the Australasian *T. planifolium*.

##### ENDOTRICHELLA ELEGANS (Doz. & Molk.) Fleisch.

Bettotan, near Sandakan, 12 Aug. 1927 ; coll. C. Boden Kloss (19101). Tenompok, Brit. N. Borneo, 1,425 m., 11 Nov. 1931 ; coll. Holttum (25334). Twigs of trees near torrent, under 300 m., G. Dulit, Sarawak, 6 Aug. 1932 ; coll. Oxford Exped. (1138).

*ENDOTRICHELLA SARAWAKENSIS* Broth.

Twigs of undergrowth trees in rain-forest, under 300 m., G. Dulit, Sarawak, 6 Aug. 1932 ; coll. Oxford Exped. (1139). Ibidem, near base of tree in 'heath forest', under 300 m., Forest Reserve, Marudi, Nov. 1932 (2608).

I think it is doubtful whether this be really specifically distinct from *E. lanceolata* C. H. Wright. The cells slightly wider seem the only definite character.

*ENDOTRICHELLA ASSIMILIS* Broth.

On tree by torrent, under 300 m., Dulit Trail, Sarawak, 30 Aug. 1932 ; coll. Oxford Exped. (1546 b). In small quantity.

I have not been able to see a specimen of the original. The present one agrees with the description in everything except that the cells are somewhat incrassate, which they are stated not to be by Brotherus. The plant is so distinct, however, from all the other species that I think it can hardly be separated on that ground alone.

*ENDOTRICHELLA PERPLICATA* Broth.

In shining, bright green tufts, c. 1,300 m., Dulit Ridge, Sarawak, 17 Sept. 1932 ; coll. Oxford Exped. (1909). Sterile. A form with long, glossy, often undulate leaves. No. 20324, Herb. Bur. Sci. Manila, det. Brotherus, is a very similar form.

New to Borneo. *Distr.* Philippines.

## METEORIACEAE.

*PAPILLARIA FUSCESCENS* (Hook.) Jaeg. var. *RIGIDICAULIS* Fleisch.

Between Lumu-Lumu and Tenompok, Brit. N. Borneo, 1,425–1,700 m., 12 Nov. 1931 ; coll. Holttum (25684, 25687).

*METEORIUM MIQUELIANUM* (C. M.) Fleisch.

Kamborangah, Brit. N. Borneo ; 17 Nov. 1931 ; coll. Holttum (1). A robust form with distant branches and the hair-points often very long, which I presume to be the form described as *Papillaria lonchotricha* C. M. Tenompok, Brit. N. Borneo, 1,425 m., 7 Nov. 1931 ; coll. Holttum and Tenompok, 1,525 m., coll. J. & M. S. Clemens, Herb. Hort. Bot. Bog. (2940). Both these are a fine robust form with yellow, turgid, julaceous branches.

*FLORIBUNDARIA FLORIBUNDA* (Doz. & Molk.) Fleisch.

Numerous gatherings, showing considerable diversity of forms.

*FLORIBUNDARIA AUREA* (Griff.) Broth.

Buttresses of tree in rain-forest, 900–1,000 m., G. Laiun, Sungei Balapau, Ulu Tinjar, Sarawak, 2 Nov. 1932 ; coll. Oxford Exped. (2369).

This species, of wide distribution, does not appear to have been hitherto recorded from Borneo.

*BARBELLA DECIPIENS* Dix., sp. n. (Pl. 2, fig. 23.)

§ *Dicladiella*.

*Stirps pulcherrima, formas pendulas B. enervis similans* ; caules secundarii ramos breves *densiuscule pinnatim* dispositos, foliis *confertis* patentibus, gerentes, nuper in ramos *praelongos*, 20 cm. vel ultra longos, pendulos, flexuosos, distanter ramulosos, producti. Folia autem toto coelo ab illa specie aliena, eis formarum graciliorum *Aerobryopsis longissimae* persimilia ; e basi *cordata amplexicauli* sensim lanceolata, inde tenui-acuminata, marginibus *valde undulatis*, arcte tenuiter denticulatis ; costa *tenuissima, distincta*, ad medium folium vel paullo ultra producta. *Areolatio tenerrima, perpellucida*, e cellulis *angustissime lineari-bus*, dorso sparsim, oblique, seriatim, *tenerrime sed alte spiculoso-papillois* ; inferiores laeves, alares *nullae*. Folia ramorum pendulorum subsimilia, in subulam longam, *capillarem*, flexuosam, producta.

Fructus ignotus.

*Hab.* Twigs of shrub in 'heath forest', c. 1,000 m., Ulu Koyan, G. Dulit, Sarawak, 7 Nov. 1932 ; coll. Oxford Exped. (2503).

A very marked species, in habit resembling forms of *B. enervis*, having long pendulous stems and branches a foot in length, but with very different leaves, which closely resemble those of slender species of *Aerobryopsis* in their form, undulate margins, the thin, single, long nerve, and the pellucid, highly spiculate cells, which, however, are extremely long and narrow, not rhomboid as there.

The Japanese *B. kiusiuensis* Broth. resembles it in many of these characters, but has a different habit, shorter and less markedly papillose cells, &c.

*AEROBRYOPSIS LONGISSIMA* (Doz. & Molk.) Fleisch.

Creeping on wood in rain-forest, G. Balapau, Ulu Tinjar, Sarawak, 2 Nov. 1932 ; coll. Oxford Exped. (2392), a form with the leaves regularly longitudinally plicate. On shrubs in undergrowth of shady moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 20 Sept. 1932 ; coll. Oxford Exped. (2000), with numerous large turgid ♂ flowers.

*AEROBRYIDIUM CRISPIFOLIUM* (Broth. & Geh.) Broth.

Near Menetendok, 920 m., 19 Nov. 1931 ; coll. Holttum (25654) ; and Tenompok, 1,325 m., 7 Nov. 1931 (25657).

New to Borneo. *Distr.* New Guinea.

A remarkable plant, robust and turgid, with the leaves very strongly undulate to base.

Brotherus has described an allied species from Borneo, *A. longicuspis*, but that has the leaves undulate only above and numerous alar cells, which here are wanting.

## NECKERACEAE.

*NECKEROPSIS GRACILENTA* (Lac.) Fleisch.

Twigs in undergrowth of rain-forest, under 300 m., G. Dulit, Sarawak, 4 Aug. 1932 ; coll. Oxford Exped. (1119). A flagelliferous form.

## NECKEROPSIS PLAGIOCHILOIDES Dix., sp. n. (Pl. 4, fig. 55.)

Gracilis ; sordide viridis ; caules *praelongi*, 25 cm. longi, flexuosi, *molles*, intertexti, remote, subregulariter pinnati ; rami divergentes, c. 1 cm. longi, percomplanati, circa 3 mm. lati, obtusi. Folia disticha, *laxa*, haud undulata, nitidiuscula, *oblonga-cultriformia*, circa 2 mm. longa, 0.75 mm. lata, e basi angustiore sensim latiora, asymmetrica, uno latere convexo, altero concavo, supra obtusissima, plano-rotundata, late obtuse apiculata, apice arete minute irregulariter denticulato, ceterum integra, uno margine ad basin late inflexo. Costa valde variabilis, *tenuis*, sed saepe *latiuscula*, male delimitata, circa medium folium vel supra soluta, foliis rameis saepe indistincta. Cellulae parvae, rhomboideae, sigmoideae, *pellucidae*, apice breviores, rhomboideae, inferne sensim elongatae, basilares lineares.

Fructus ignotus.

*Hab.* On log in river, subject to submergence, under 300 m., Sungei Balapau, Tinjar, Sarawak, 15 Oct. 1932 ; coll. Oxford Exped. (2235).

A fairly well-marked species in habit and structure. *N. borneensis* Fleisch. is *e descr.* more robust, with the leaf-apex entire or nearly so, the leaves more or less undulate or plicate when dry, etc. The leaves here are neither rugulose nor plicate when dry, but almost unaltered, sometimes slightly deflexed on each side, and being narrow and somewhat distant they suggest species of *Plagiochila*.

## NECKEROPSIS LEPINEANA (Mont.) Fleisch.

Dallas, Brit. N. Borneo, c. 1,000 m., 6 Nov. 1931 ; coll. Holttum (25345). In deep shade, Niah (IVth Division), c. 300 m., on damp limestone crags outside caves, Sarawak ; coll. P. M. Syngé, Oxford Exped. (593).

## HIMANTOCLADIUM CYCLOPHYLLUM (C. M.) Fleisch.

Boulder by torrent, under 300 m., G. Dulit, Sarawak, 8 Aug. 1932 ; coll. Oxford Exped. (1165).

## HOMALIODENDRON FLABELLATUM (Dicks.) Fleisch.

From several localities.

## HOMALIODENDRON MICRODENDRON (Mont.) Fleisch.

Tenompok, 1,220 m., Brit. N. Borneo, 17 June 1925 ; coll. C. M. Enriquez (18112). Rain-forest on crest of ridge, 700–800 m., G. Balapau, Ulu Tinjar, Sarawak, 2 Aug. 1932 ; coll. Oxford Exped. (2,390, p.p.). Tabekang, Sadong, Sarawak, Feb.–June 1914 ; Herb. Bur. of Sci., Manila (2507).

## HOMALIODENDRON FLEISCHERI Dix.

Sungei Blooeoe, Borneo, 1896–7 ; coll. Jaheri (1120), Herb. Hort. Bot. Bog. (2020).

Not, I believe, collected since the original gathering at Tenom.

**PINNATELLA AMBIGUA** (Bry. jav.) Fleisch.

Kiau, W. Koetai, Oct. 1925 ; coll. F. H. Endert (4648), Herb. Hort. Bot. Bog. (2570 b).

**PINNATELLA ANGUSTINERVIS** Dix., sp. n.

Gracilis. Habitu formarum minorum *P. mucronatae* ; frondes bipinnati, complanati. Stipitis folia parva, valde deflexa. Folia parva, concava, late ovalia, subobtusata vel late acuta, vel brevissime apiculata, *pellucida, integra vel minutissime crenulata* ; *costa tenuissima, medio folio soluta, saepe brevior*. Cellulae breviter ovoides, vel ovato-rhomboides, apice paullo breviores, brevissime rhomboides, basilares elongatae, lineares, omnes laeves.

Cetera ignota.

*Hab.* Baram, N.W. Borneo ; coll. A. H. Everett, Herb. Mitten, in Herb. N.Y. Bot. Garden.

Very near to *P. mucronata* (Bry. jav.), and possibly scarcely specifically distinct. It is, however, more slender, less densely branched ; the leaves which there are irregularly erose-denticulate at the apex are here entire or only minutely crenulate-denticulate ; and the cells are more elongate. In *P. mucronata* all the apical cells and frequently most of the upper ones are isodiametric ; here that appears never to be so, even the apical ones being slightly longer than broad.

#### SYMPHYODONTACEAE.

**SYMPHYODON PERROTTETII** Mont.

Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931 ; coll. Holttum (25680). A pendent, densely interwoven form. I have a similar plant from Ceylon.

New to Borneo. *Distr.* South India ; Ceylon ; Java ; Halmaheira ; Ceram. The first species of this interesting genus to be recorded from the island.

#### NEMATACEAE.

**EPHEMEROPSIS TJIBODENSIS** Goeb.

Leaves of herb in rain-forest, in small stream valley, c. 500 m., Dulit Trail, Sarawak, 9 Aug. 1932 ; coll. Oxford Exped. (1183), the ♂ plant. On leaf of shrub in rain-forest, c. 1,200 m., Dulit Ridge, Sarawak, 13 Sept. 1932 ; coll. Oxford Exped. (1879), an unusually lax form. Tenompok, Brit. N. Borneo, 1,425 m., 11 Nov. 1931 ; coll. Holttum (25699), the ♂ plant. Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931 ; coll. Holttum (25698).

New to Borneo. *Distr.* Java ; Sumatra ; Malay Penins. ; Siam ; Laos ; New Guinea ; New Zealand

#### HOOKERIACEAE.

**LESKEODON ACUMINATUS** (Doz. & Molk.) Fleischer

On wet sandstone rocks by waterfall, c. 1,230 m., Dulit Ridge, Sarawak. 19 Sept. 1932 ; coll. Oxford Exped. (1973).



## DISTICHOPHYLLUM JUNGERMANNIODES (C. M.) Bry. jav.

Sandstone rocks in spray of torrent, c. 500 m., G. Dulit, Sarawak, 17 Nov. 1932; coll. Oxford Exped. (2609).

New to Borneo. *Distr.* Java; Sumbawa.

An interesting extension of the range of this minute and peculiar little species.

## DISTICHOPHYLLUM DENTICULATUM Dix., sp. n. (Pl. 3, fig. 27.)

*D. Osterwaldii* Fleisch. affine, sed *multo minus*. Caulis ut videtur brevis, frons circa 3 mm. lata (nec 7–9 mm. ut in illa specie); folia lateralibus tantum 2–2.25 mm. longa (in *D. Osterwaldii* 4–5 mm.); cellulae pellucidiores, minores, apud apicem costae 13–16  $\mu$  latae, marginales 7–10  $\mu$ ; limbus *angustissimus*, apud folii basin 2-seriatus, reliquo uniseriatus, versus apicem folii aut omnino carens aut interrupte indistincte evolutus. Margines superiores, *per tertiam folii partem, sat fortiter, irregulariter denticulati*.

Setae fragmentum tantum visum, acete sed haud alte papillosum.

*Hab.* Sarawak, coll. Everett, Herb. Mitten, ex herb. New York Bot. Gard.

Only a few stems received, with a fragment of seta. The leaves are more strongly denticulate than in any species with which I am acquainted, and the denticulation descends far down the margin. The leaves are elongate-spathulate as in *D. Osterwaldii*, and as in that show considerable variation in the apex, which is broadly rounded, but may be quite obtuse or slightly obtusely pointed. In *D. Osterwaldii* the border disappears about mid-leaf; here traces may be seen even at the apex.

## DISTICHOPHYLLUM ANGUSTIFOLIUM Dix., sp. n. (Pl. 2, fig. 25.)

Humillimum; inter alios muscos sparse crescens; *albescens*, molle. Folia *mollissima, lingulato-spathulata, complanata*, 2.5–3 mm. longa, 0.75–0.8 mm. lata, *perpellucida*, e basi angusta sensim latiora, apice paullo angustato, late acutato, *valide, oblique apiculato*. Margines integerrimi, undulati, limbo *angustissimo* 1–2-seriato hyalino circumdati. Costa pertenuis, *brevis*, dimidiam partem folii vix superans. Cellulae *perpellucidae*, inanes, laxae, hexagonae, saepe paullo elongatae, media lamina, ubi latissima, 30–40  $\mu$  latae, versus marginem paullo minores, parietibus tenuibus, firmis, basilares pertenues, elongatae.

Seta circa 5 mm. longa, curvata, ubique *dense, altissime, hispidulo-papillosa*; bracteae ovatae, laxae areolatae, molles, vaginula duplo longiores; theca horizontalis, ovalis; peristomium magnum, pallidum. Calyptra haud visa.

*Hab.* Lobang, Brit. N. Borneo, 1,220 m., 19 Nov. 1931; coll. Holttum (25638 b).

Growing in small quantity with *D. undulatum* Doz. & Molk. A small but very striking species, quite distinct from any other; in the form of the leaf, but in that alone, resembling *D. angustissimum* below.

## DISTICHOPHYLLUM ANGUSTISSIMUM Dix., sp. n. (Pl. 3, fig. 26.)

Humile, sordide pallide viride; folia undique patentia, haud complanata, sicca *valde tortilia, flexuosa*; e basi longa angusta *anguste lingulato-spathulata*, 3 mm. longa, 0.35 mm. lata, *concava*, saepe convoluta, apice *acutato, peracuta, cuspidato*. Limbus angustus, 2–3-seriatus, hyalinus, tenuis. Costa pro

genere latiuscula, paullo infra apicem soluta. Cellulae inanes, perpellucidae, irregulariter hexagonae, 20–25  $\mu$  latae, ad marginem vix minores, parietibus tenuibus, firmis.

Seta circa 3 mm. longa, dense hispidulo-papillosa, infra thecam incrassata; calyptra dense intricate setosa; theca minuta, erecta, castanea, ovalis; operculum e basi conica tenui-rostratum.

*Hab.* Rotten log in stream-bed, in primary forest, under 300 m., G. Dulit, Sarawak, 31 Aug. 1932; coll. Oxford Exped. (1582). In similar situation, c. 500 m. (2612).

Probably allied to *D. angustifolium*, which it resembles in the long narrow leaves; they are, however, here narrower, sharply acute and cuspidate at the apex, much contorted when dry, the cells much smaller, and the nerve stronger and much longer.

#### DISTICHOPHYLLUM CUSPIDATUM Doz. & Moll.

On small tree near ground in sandy forest, c. 950 m., Ulu Koyan, Sarawak, 15 Sept. 1932; coll. Oxford Exped. (1852). On stem of shrub in shady moss forest, c. 1,300 m., Dulit Ridge, Sarawak, 17 Sept. 1932; coll. Oxford Exped. (1912).

New to Borneo. *Distr.* Wide.

#### DISTICHOPHYLLUM ACIPHYLLUM Dix., sp. n. (Pl. 2, fig. 24.)

*D. borneënsi* Broth. proximum; differt statura minore, caulibus brevissimis, dense compactis, foliis minoribus, lateralibus 1.5 mm. longis, 0.4 mm. latis (*D. borneënsis* 2 mm. longis, 0.8 mm. latis), apice acute angustatis, in cuspidem validam curvatam sensim acutatis; costa multo brevior, tenuior; cellulis paullo majoribus, 13–18  $\mu$  latis, pellucidioribus.

*Hab.* Foot of G. Damoes, Borneo, 1893–4; coll. H. Hallier (449), Herb. Hort. Bot. Bog. (2017 c).

Although very near to *D. borneënsis* this is certainly distinct. It is much smaller, with leaves of a different form; in that they are oblong-spathulate from a narrower base, and abruptly obtusely rounded at the apex, with an acute, abrupt, cuspidate point. Here they are obovate from a spathulate base, and gradually narrowed from the widest part to an acute point, which is continued into the stouter, longer, curved cusp. The nerve in *D. borneënsis* ceases some way below the point, as in most species, where the leaf has already begun to narrow; here it ceases much lower, at the broadest part of the leaf; and the cells are appreciably larger and more pellucid. The leaves are more or less twisted, both moist and dry. It is also much like *Leskeodon acuminatus*, and may belong to that genus, but the leaves are much broader and shorter in proportion and the nerve much shorter.

#### DISTICHOPHYLLUM MITTENII Bry. jav.

On rock by stream, c. 1,070 m., near Dallas, 5 Nov. 1931; coll. Holttum (25266 c).

New to Borneo. *Distr.* Wide; Ceylon to New Caledonia.

*DISTICHOPHYLLUM UNDULATUM* Doz. & Molk.

Lobang, Brit. N. Borneo, 1,220 m., 19 Nov. 1931; coll. Holttum (25638).  
New to Borneo. *Distr.* New Guinea; Java; Sumatra; Malay Penins.

*DISTICHOPHYLLUM PERUNDULATUM* Dix., sp. n.

Sat robustum, atro-viride; caules usque ad 3 cm. alti, *laxifolii*; folia lateralalia 3 mm. longa, 1 mm. lata, e basi angusta oblonga, sicca *valde undulata*, apice late rotundato, *fortiter apiculato, seu breviter cuspidato*. Costa basi validiuscula, supra attenuata, *prope apicem soluta*. Cellulae sat magnae, media lamina superiore circa  $20\mu$  latae, versus costam latiores, versus marginem sensim multo minores, marginales circa 8–10  $\mu$  latae, omnes indistincte collenchymaticae. Limbus folii *validus*, prope basin usque ad 40  $\mu$  latus, supra paullo angustior, integerrimus.

Fructus ignotus.

*Hab.* On wet sandstone rocks in forest, c. 1,000 m., Ulu Koyan, Sarawak, 15 Sept. 1932; coll. Oxford Exped. (1863).

Marked in the extremely undulate leaves when dry, the stout border continued without much diminution to the apex, the broadly rounded apex with strong oblique apiculus, and the rather unusually long nerve, which often reaches nearly to the apex, and in one instance was seen actually reaching to the tip.

*DISTICHOPHYLLUM OSTERWALDII* Fleisch.

Wet sandstone rocks by small forest stream, under 300 m., G. Dulit, Sarawak, 2 Sept. 1932; coll. Oxford Exped. (1605).

New to Borneo. *Distr.* Java; Philippines; ? Malay Penins.

The plant recorded from the Peninsula (Robinson's Falls, Cameron's Highlands, coll. Holttum, 23263) differs slightly in the nerve reaching nearly to the apex, the slightly better developed border, and the leaves highly undulate, and may perhaps belong to a different species.

*ERIOPIUS REMOTIFOLIUS* C. M.

On rotten log in shady moss forest, c. 1,300 m., Dulit Ridge, Sarawak, 17 Sept. 1932; coll. Oxford Exped. 1932 (1907).

*CALLICOSTELLA PAPILLATA* (Mont.) Jaeg.*CALLICOSTELLA PRABAKTIANA* (C. M.) Bry. jav.

Several gatherings of these two common species were made.

*HOOKERIOPSIS UTACAMUNDIANA* (Mont.) Broth.

Between Tenompok and Lumu-Lumu, Brit. N. Borneo, 1,425–1,700 m., 12 Nov. 1931; coll. Holttum (25321), c.fr.

New to Borneo. *Distr.* Sikkim; South India; Ceylon; Sumatra; Java; New Guinea.

## CHAETOMITRIUM Doz. &amp; Molk.

Borneo and New Guinea would seem to be respectively the headquarters of this remarkable genus. Of about thirty-five species known, thirteen are known from Borneo and fourteen from New Guinea. Certain groups are very perplexing, and it seems scarcely possible to distinguish one or two of the species without fruit. Among the species listed below, *C. bornense* and *C. setosum* by the habit and large size, *C. horridulum* by its robust habit and colour, and *C. leptopoma* by its small dense growth are easily recognized. It may be of some help to give a key to the remaining species, including one or two which occur in Borneo, but not included in the present list.

All the species of the genus appear to be inhabitants of the lower slopes of mountains; most of those listed here were from below 300 m.; Fleischer gives very few localities for the Javan species above 1,500 m., *C. ciliatum* being the only species which appears to range about 2,000 m. They are generally or always corticolous or epiphyllous.

## Key.

- |       |  |                        |
|-------|--|------------------------|
| 1. {  | Calyptra cucullate . . . . .   | 2.                     |
|       | Calyptra mitriform. . . . .  | 3.                     |
| 2. {  | Calyptra subentire at base, seta papillose above . . . . .                                 | <i>lanceolatum.</i>    |
|       | Calyptra longly fringed, seta papillose to base . . . . .                                  | <i>cucullatum.</i>     |
| 3. {  | Leaves smooth at back . . . . .  | 4.                     |
|       | Leaves more or less spiculose at back . . . . .  | 5.                     |
| 4. {  | Leaves acutely pointed, entire, small, dense plant . . . . .                               | <i>fimbriatum.</i>     |
|       | Leaves shortly and widely pointed, more robust and laxer . . . . .                         | <i>Warburgii.</i>      |
| 5. {  | Leaves toothed from the base . . . . .   | 6.                     |
|       | Leaves toothed above only . . . . .  | 8.                     |
| 6. {  | Cells almost smooth at back . . . . .  | <i>torquescens.</i>    |
|       | Cells markedly spiculose . . . . .   | 7.                     |
| 7. {  | Leaves very acute, weakly toothed . . . . .  | <i>papillifolium.</i>  |
|       | Leaves bluntly pointed, densely toothed throughout, upper teeth often bigeminate . . . . . | <i>Everettii.</i>      |
| 8. {  | Calyptra fringed at base . . . . .   | 9.                     |
|       | Calyptra without basal fringe . . . . .  | <i>ciliatum.</i>       |
| 9. {  | Seta papillose above . . . . .   | <i>elongatum.</i>      |
|       | Seta hispidulose above . . . . .   | 10.                    |
| 10. { | Leaves sparsely papillose . . . . .  | <i>orthorrhynchum.</i> |
|       | Leaves strongly and highly papillose . . . . .   | <i>Beccarii.</i>       |

CHAETOMITRIUM LEPTOPOMA (Schwaegr.) Bry. jav.

Kinabalu, 1932; coll. J. & M. S. Clemens, Herb. Hort. Bot. Bog. (2969 *b*).  
New to Borneo. *Distr.* Java; Malay Penins.

CHAETOMITRIUM WARBURGII Broth.

Dallas, Brit. N. Borneo, 915 m., 6 Nov. 1931; coll. Holttum (25280 *a*).  
New to Borneo. *Distr.* Philippines.

**CHAETOMITRIUM FIMBRIATUM** (Doz. & Molk.) Bry. jav.

On tree by torrent, under 300 m., Dulit Trail, Sarawak, 30 Aug. 1932; coll. Oxford Exped. (1546).

New to Borneo. *Distr.* Amboina; New Guinea. (The authors of the Bry. jav. say that they have not seen the Bornean plant. But Dozy and Molkenboer record it from Amboina, not from Borneo.)

**CHAETOMITRIUM TORQUESCENS** Bry. jav.

Tree-trunks near ground in rain-forest, c. 900 m., Ulu Koyan, Sarawak, 7 Nov. 1932; coll. Oxford Exped. (2531).

New to Borneo. *Distr.* Java; Amboina; Ceram; Siam; New Guinea.

**CHAETOMITRIUM ORTHORRHYNCHUM** (Doz. & Molk.) Bry. jav.

Shrub in forest, under 300 m., G. Dulit, Sarawak, 17 Aug. 1932; coll. Oxford Exped. (1320). Twigs of shrub in secondary forest, *ibidem*, 14 Aug. 1932 (1265). *Ibidem*, 6 Aug. 1932 (1137). Upper Sarawak; coll. Everett (?); Herb. Mitten.

**CHAETOMITRIUM BECCARII** Dix., sp. n. (Pl. 3, fig. 29.)

*C. orthorrhyncho* Bry. jav. affine et similitum. Differt foliis atque bracteis perichaetii dorso *alte, spiculose, fortiter papillosis*.

*Hab.* Epiphyllous, foot of Damoes, Borneo, 1893-4; coll. Hallier (449), Herb. Hort. Bot. Bog. (2017 b). O. Beccari, *Crittogame di Borneo*, no. 16, Sarawak, Mtn. Mattan, 1862 (Herb. Hampe in Herb. Mus. Brit., sub nom. *C. orthorrhynchum*), type.

The highly spiculate cells appear to be the only differentiating character from the Javan *C. orthorrhynchum*, but this appears to be constant and extremely marked. The fruiting characters seem to present no differences, but I have seen no calyptra of *C. Beccarii*.

**CHAETOMITRIUM CUCULLATUM** Dix., sp. n.

E minoribus generis, habitu *C. papillifolii* et *C. lanceolati*; folia caulina breviter cuspidata, ramea breviter acute acutata, *haud vel raro sub apice constricta, breviuscule denticulata*; cellulae pellucidae, *laeves vel sparsim humillime spiculosae*. Propagula filamentosa hyalina axillis foliorum superiorum *dense aggregata*. Perichaetii bractae internae erectae, subtruncatae, *laceratae*, inde breviter subulatae, ciliato-denticulatae. Seta circa 1 cm. alta, *ubique dense alte papillosa*. Calyptra cucullata, superne hispida, infra longe ciliata. Theca inclinata, e collo brevi oblongo-elliptica, castanea, laevis, majuscula.

*Hab.* Rotten log in rain-forest, G. Balapau, Ulu Tinjar, Sarawak, 2 Nov. 1932; coll. Oxford Exped. (2395).

Similar to *C. lanceolatum* and *C. papillifolium* in the leaves, not or scarcely constricted below the apex, but rather gradually tapering, and in the cells almost smooth at the back; from all the allied species in the cucullate calyptra longly fringed at the base, and the seta papillose throughout. The crowded brood-filaments are similar to those in *C. papillifolium* and *C. nematosum*.

*CHAETOMITRIUM HORRIDULUM* Bry. jav.

On shrub in 'heath forest', c. 800 m., Ulu Koyan, Sarawak, 22 Sept. 1932; coll. Oxford Exped. (2030).

New to Borneo. *Distr.* Java.

A fine and rare species. It is variegated with dull purple, which appears to be a specific character.

*CHAETOMITRIUM CILIATUM* Bry. jav.

Leaves of small tree in rain-forest, under 300 m., G. Dulit, Sarawak, 4 Aug. 1932; coll. Oxford Exped. (1120).

New to Borneo. *Distr.* Java.

*CHAETOMITRIUM EVERETTII* Mitt. MS. in herb., sp. n. (Pl. 3, fig. 28.)

Sat robustum, elongatum, pallide viride. *C. papillifolio* Bry. jav. forsan proximum, differt habitu laxiore, molliore; caulibus flexuosis, *inaequaliter, laxius* pinnatis, foliis majoribus, circa 1 mm. longis, *laxius* dispositis, substrictis, saepe horizontaliter patentibus, sub acumine distincte constrictis, marginibus *conferte, pulchre regulariter*, superne *bigeminatim*, e basi fere pellucide denticulatis. Cellulae pellucidae, dorso dense, acute, nec alte spiculosae; versus basin seriebus paucis laxiores; costae binae brevissimae vel nullae. Folia eis *C. orthorrhynchi* (Doz. & Molk.) sat similia, sed *longiora, angustiora, strictiora*, minus concava, *brevius, arctius denticulata*.

Fructus caret.

*Hab.* Baram, Brit. N. Borneo, Sept. 1892; coll. A. H. Everett, Herb. Mitten, ex herb. New York Bot. Gard.

Although without fruit, this may I think safely be described as new. It is much laxer, less densely branched and foliate than the smaller species, but slender and more laxly foliate than *C. philippinense*, *C. elongatum*, &c. The leaves are more or less seriate, the lateral ones standing out almost horizontally from the stem, stricter and less concave than most of the species having the peculiar constriction below the apex characteristic of many of the species of the genus. The denticulation of the leaves is marked, being very close, very equal from base to apex, and in the upper part bigeminate.

*CHAETOMITRIUM BORNENSE* Mitt.

Samarang River, near Sandakan, 12 July 1927; coll. C. Boden Kloss (18694).

*CHAETOMITRIUM SETOSUM* Broth.

Twigs and leaves of small tree in rain-forest, near torrent, under 300 m., G. Dulit, Sarawak, 7 Aug. 1932; coll. Oxford Exped. (1144).

*DIMORPHOCLADON BORNEËNSE* Dix.

On palm leaf in undergrowth of forest by torrent, under 300 m., G. Dulit, Sarawak, 12 Nov. 1932; coll. Oxford Exped. (2566, 2569).

This interesting species has been found by Dr. Kerr in Siam.

## RHACOPILACEAE.

*RHACOPILUM SPECTABILE* Hornsch. & Reinw.

In numerous gatherings.

## HYPOPTERYGIACEAE.

*CYATHOPHORUM SPINOSUM* (C. M.) Fleisch.

Tree-trunk near ground, primary forest, c. 500 m. alt., Dulit Trail, Sarawak, 27 Aug. 1932; coll. Oxford Exped. (1512).

New to Borneo. *Distr.* Java; Moluccas; Siam; New Guinea; New Hebrides.

*HYPOPTERYGIUM VRIESEI* Bry. jav.

Borneo, 1896-7; coll. Jaheri, Exped. Nieuwenhuis, Herb. Hort. Bot. Bog. (2563 b).

New to Borneo. *Distr.* Java; Sumatra; Amboina; Ceram; Philippines; New Guinea.

*HYPOPTERYGIUM CEYLANICUM* Mitt.

Tenompok, Brit. N. Borneo, 1,220 m., 17 June 1925; coll. C. M. Enriquez, Herb. Singapore Bot. Gard. (11815). On boulder in bed of torrent in moderate shade, under 300 m., Dulit Trail, Sarawak, 3 Aug. 1932; coll. Oxford Exped. (1117). Branch of shrub in forest, under 300 m., G. Dulit, Sarawak, 12 Nov. 1932; coll. Oxford Exped. (2553). The two last show a robust form, with the stipes leaves often squarrose, and the nerve of the amphigastria strong and reaching above the middle. I think, however, it can be considered only a form of *H. ceylanicum*.

New to Borneo. *Distr.* South India; Ceylon; Sumatra; Java; Buru; Philippines; New Guinea.

## LESKEACEAE.

*PSEUDOLESKEOPSIS ZIPPELII* (Doz. & Molk.) Broth.

Kadamaian River, near Menetendok, Brit. N. Borneo, 900 m., 19 Nov. 1931; coll. Holttum (25192).

## • THUIDIACEAE.

*PELEKIMUM VELATUM* Mitt.

In several gatherings.

*THUIDIUM PLUMULOSUM* (Doz. & Molk.) Bry. jav.

Kabayan, Brit. N. Borneo, 150 m., on rock in rocky glen, 13 June 1925; coll. C. M. Enriquez, Herb. Singapore Bot. Gard. (18101). Between Kundin baru and Batu babi, South-east Borneo, 8 July 1908; coll. Hubert Winkler (2773), c.fr.

*THUIDIUM GLAUCINUM* (Mitt.) Bry. jav.

Tenompok, Brit. N. Borneo, 1,425 m., 11 Nov. 1931; coll. Holttum (25324 c). This has the papillae sometimes entire, sometimes forked.

**THUIDIUM GLAUCINOIDES** Broth.

Rain-forest on crest of ridge, 700–800 m., G. Balapau, Ulu Tinjar, Sarawak, 2 Nov. 1932; coll. Oxford Exped. (2390). A form with very low papillae.

**THUIDIUM CYMBIFOLIUM** (Doz. & Molk.) Bry. jav.

In several gatherings.

**BRACHYTHECIACEAE.****RHYNCHOSTEGIELLA OPACIFOLIA** Dix., sp. n. (Pl. 3, fig. 30.)

Caespites densi sed facilliter dilabiles, *fusci*, caules prostrati, dense ramosi, ramis erectis, longis (1 cm. vel ultra), robustiusculis. Folia sat conferta, erecto-patentia vel leniter secunda, majuscula, caulina 1–1.25 mm. longa, 0.4 mm. lata, ovato-lanceolata, saepe convoluta, late breviter acuminata, *obtusae*; ramea minora, magis ovalia; omnia sicca plus minusve anguste convoluta; margines plani, a parte inferiore folii ad apicem *arcte, subobtusae, pellucide* denticulati. Costa validiuscula, superne attenuata, supra medium folium soluta. Cellulae *peropacae, angustissimae, parietibus tenuibus obscuris*; marginales saepe *pellucidiores*; versus basin paullo latiores, infimae subrectangulares, alares *paucae vel nullae, omnes obscurae*.

Autoica. Perichaetium parvum, bracteis paucis, e basi lata cito in acumen flexuosum subulatum integrum constrictis. Seta 1.25 cm. alta vel paullo ultra, *laevis*. Theca turgide ovalis, sicca deoperculata angustior, asymmetrica, inclinata, pachydermica, saturate fusca, deoperculata 1.5 mm. longa; operculum curvirostratum.

*Hab.* Long Hoet, W. Koetai, Borneo, Aug. 1925; coll. F. H. Endert (2631), Herb. Hort. Bot. Bog. (2521), type. S. Mesoemai, Djambi, Sumatra, July 1925; coll. O. Posthumus (527 a); Herb. Hort. Bot. Bog. (2529).

The type appears to have been growing in sandy soil, the Sumatran plant in very extended cushions on small branches, both probably near water. The leaves are always brown, of a very opaque and obscure texture, widely pointed and often obtuse, the alar cells very few and very obscure.

Nearest perhaps to *R. ovalifolia* Dix. from Siam, but that has quite different cells, and leaves very slightly denticulate. *R. Edanoi* Broth. from the Philippines has leaves acutely pointed and longer rough seta.

The genus *Rhynchostegiella* is difficult to define, and in the second edition of the 'Musci' Brotherus has transferred to *Rhynchostegium* several species, allied to *R. menadense* (Bry. jav.), previously described or placed under *Rhynchostegiella*. Among these the present plant is nearest to *R. menadense*, but has non-complanate leaves, more strongly serrulate and much smaller, very obscure cells. The leaves, convolute and subtubular when dry, are similar to those of other species of *Rhynchostegiella*, and appear to me to give a character of some importance.



*RHYNCHOSTEGIUM JAVANICUM* (Bél.) Besch.

Below Dallas, Brit. N. Borneo, 1,000 m., 6 Nov. 1931 ; coll. Holttum (25281).  
A form with rather weak, variable nerve.

This very widely spread species does not appear to have been recorded from Borneo.

## HYLOCOMIACEAE.

*MACROTHAMNIUM JAVENSE* Fleisch.

Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931 ; coll. Holttum (25540).

*RHIZOHYPNELLA SUNDAËNSIS* Fleisch.

Base of large tree in primary forest, c. 500 m., Dulit Trail, Sarawak, forming a deep green carpet, 26 Aug. 1932 ; coll. Oxford Exped. (1513). Base of large tree in rain-forest, 900–1,000 m., G. Laiun, S. Balapau, Ulu Tinjar, Sarawak, 2 Nov. 1932 ; coll. Oxford Exped. (2371). Both fruiting.

New to Borneo. *Distr.* Java.

Hitherto known only from a single station in Java.

*CTENIDIADELPHUS SPINULOSUS* (Broth.) Fleisch.

Bongaya, 1898 ; coll. Ridley (837). Rotten trunk in primary forest, under 300 m., G. Dulit, Sarawak, 22 Aug. 1932 ; coll. Oxford Exped. (1421). Rain-forest on high ridge, G. Laiun, Sungei Balapa, Ulu Tinjar, Sarawak, 2 Nov. 1932 ; coll. Oxford Exped. (2372).

I greatly doubt whether the Borneo plant be distinct from the Javan *C. Plumularia*.

## SEMATOPHYLLACEAE.

*PTYCHOPHYLLUM BORNEËNSE* Broth. (*Ptychophyllum aureum* Dix. & Herz.).

On shrubs, trunks, and rotten logs in shady moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 20 Sept. 1932 ; coll. Oxford Exped. (2001). Ibidem, 13 Aug. 1932 (1785 c). The former specimen is a very fine one, pale yellow, with stems 10–15 cm. long, regularly pinnately branched, the branches subequal, about 8 mm. long. The other showed a few stems only, mixed with other mosses. No fruit was seen.

The history of this plant, it may be recalled, is remarkable. Brotherus published his new genus in 1928, based on a specimen of Everett's from Sarawak and one of Joh. Winkler's from West Borneo. Quite independently and almost simultaneously we published our new genus of the same name, from a specimen collected in East Borneo by Dr. Balneti. The two proved to be identical species ! It has, I believe, not been found elsewhere. Unfortunately perfect fruit has not been seen. Brotherus places it with hesitation as near *Ctenidium* ; I incline to think it near *Acanthocladium* and *Trismegistia*.

## MASTOPOMA Card.

This interesting genus has its headquarters in Borneo. Brotherus in his paper (7) has added five new species to the three already known, which, with the new species described below and an unpublished species from Malaya, makes a total of ten, only two of which are not known from Borneo. To these, moreover, may probably be added the Bornean *Hypnum salaëense* Hampe, which, as I have stated below, appears to belong to this genus rather than to *Trismegistia*.

MASTOPOMA UNCINIFOLIUM (Broth.) Card. (*Warburgiella armata* Broth.).

N.E. Borneo; coll. Burbidge, Herb. Mitten. Matang, Borneo; coll. Everett, Herb. Mitten. Santubong, Borneo; coll. Everett (probably), Herb. Mitten. Kinabalu; coll. Burbidge, Herb. Mitten. All these were in Mitten's herbarium as '*Acanthocladium*'. Lumu-Lumu, Kinabalu, 18 June 1925, coll. C. M. Enriquez, Herb. Singapore Bot. Gard. (18130 *b*). Between Lumu-Lumu and Kamborangah, 1,700–2,200 m., 13 Nov. 1931; coll. Holttum (25319). Kemoel, W. Koetai, coll. F. H. Endert (4470, 4540), Herb. Hort. Bot. Bog. (2527, 2588).

This varies considerably in size, but is generally easily recognizable by the strongly falcate, longly and narrowly acuminate leaves.

*Warburgiella armata* Broth. is, from original specimens, certainly this.

## MASTOPOMA PAPILLOSUM Broth.

East Borneo, 1925; coll. Dr. Balneti, Herb. Herzog (5).

## MASTOPOMA LAEVISETUM Broth.

Near Dallas, Brit. N. Borneo, 5 Nov. 1931; coll. Holttum (25266).

## MASTOPOMA DENTICULATUM Dix., sp. n. (Pl. 3, fig. 32.)

Sordide viride, depressum. Habitu *M. uncinifolii* (Broth.) sed foliis *minime dentatis*, *apice tantum*, praecipue rameorum, dentibus *paucis*, *argutis* praeditis. Cellulae perangustae, elongatae, alares magnae, hyalinae vel hic illic aurantiacae, vesiculosae, tenerrimae, alas magnas, conspicuas formantes. Perichaetium magnum, 3 mm. vel ultra altum; bractae *strictae*, internae *erectae*, late lanceolatae, sensim in acumen *late loriforme*, *dense argute denticulatum* angustatae. Seta 2–2.25 cm. alta. Theca parva, inclinata, e collo defluente elliptica, sub ore aetate contracta, atro-fusca; calyptra longa, cucullata; operculum *breve*, conicum, apiculatum.

*Hab.* Kemoel, W. Koetai; Oct. 1925; coll. F. H. Endert (4518), Herb. Hort. Bot. Bog. (2548).

Assuming this to be a *Mastopoma*, it differs at once from all the known species in having the leaves only slightly denticulate at the apex alone. The question arises whether it might be a *Brotherella*, but the very large, hyaline, thin-walled, altogether Sematophylloid alar cells, the long seta, and the small short capsule with shortly conical lid are in favour of *Mastopoma*. If it should

be a *Brotherella* it is amply distinct from any known species. I have not seen *B. longipes* Broth., but *e. descr.* that has the perichaetial bracts 'in acumen lanceolato-subulatum attenuatae', and the lid shortly rostrate, and the seta 3.5 cm. long, as well as having the branches strongly complanate, which they are not here.

*MASTOPOMA SALAËNSE* (Hampe) Dix., comb. nov. (*Hypnum salaënsse* Hampe; *Trismegistia salaënsis* Broth.).

Kemoel, W. Koetai, Oct. 1925; coll. F. H. Endert (4470, p.p.), Herb. Hort. Bot. Bog. (2527 b). Rotten log in forest, c. 700 m., Dulit Trail, Sarawak, 27 Aug. 1932; coll. Oxford Exped. (1502). Ibidem, under 300 m., 2 Sept. 1932 (1610). The last in good fruit, which, with its long setae and short conical-apiculate lid, is quite characteristic of *Mastopoma*. Hampe's plant is little known; the specimen in his herbarium is scanty and without fruit. The distinction between *Mastopoma* and *Trismegistia* is slight, and the differences mostly resolve themselves into three; in *Mastopoma* the smaller, less rigid habit, the upper cells all elongate and not incrassate, never short and rhomboid with elongate marginal ones as is usual in *Trismegistia*, and the capsule lid conical, not rostellate nor rostrate. In all these characters Hampe's plant agrees fully with *Mastopoma*, not with *Trismegistia*.

The species is distinguished from the other Bornean ones rather markedly by the comparatively short and broad acumen of the leaves. These show a peculiarity in the toothing which is perhaps shared with other species, but is, I believe, more marked here. The upper margins are narrowly reflexed, and are fairly equally and spinulose toothed. The teeth, however, are not in the plane of the margin, but alternate to right and left, exactly as the teeth of a saw are set, though the margin is in no way thickened, as might be supposed from this. Viewed from the back of the leaf it has a very distinctive appearance.

*MASTOPOMA SUBROBUSTUM* Dix., sp. n.

*M. robustum* Broth. comparandum sed minus, *pallescens*, aureo-viride, magis pinnatum, ramis *brevioribus*, minusquam 1 cm. longis, complanatis; folia *minora*, 2 mm. longa, *minus fortiter* dentata.

Perichaetia magna, 4 mm. alta, bracteis *erectis*, flexuosis, robuste attenuatis, fortiter dentatis. Seta flexuosa, 4-5 cm. alta, theca sat parva, inclinata, elliptica, gibbosa. Operculum haud visum.

*Hab.* On tree-trunks, rotten logs, &c., in shady moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 20 Sept. 1932; coll. Oxford Exped. (2002).

The largest of all the described species, except *M. robustum* Broth., from which it differs not only in the considerably smaller size, the more complanate habit, pale colour, but also in the dentation of the leaves. Here the acumen is moderately strongly toothed, but the toothing does not descend far; in *M. robustum* the border is regularly, rather distantly, very strongly, *spinose* toothed for

a long way down, the more conspicuously because the margin is often somewhat reflexed.

The fruit of *M. robustum* is unknown.

#### TRISMEGISTIA Broth.

I find this a very perplexing genus, as the characters separating the species are rather elusive, and several of the species are highly variable. I do not feel by any means confident that all the determinations below are correct.

#### TRISMEGISTIA LANCIFOLIA (Harv.) Broth.

Numerous gatherings, very varied in habit. I place here two plants collected by the Oxford Expedition (1503 b & 1516), from low altitudes on G. Dulit, both very complanate, with lax branching, rather lax foliation, the leaves spreading, very straight and rigid.

A very fine, robust form in good fruit was collected in 'heath forest', Marudi, Baram, by the Oxford Exped. (1021), with setae up to 7 cm. in length, and capsules (operculate) 4 mm.

#### TRISMEGISTIA RIGIDA (Hornsch. & Reinw.) Broth.

In several gatherings.

#### TRISMEGISTIA PANDURIFORMIS (C. H. Wright) Broth.

Tenompok, Brit. N. Borneo, c. 1,500 m., Nov. 1931; coll. Holttum (25333, 25636). Kamborangah, 2,200 m., 17 Nov. 1931; coll. Holttum (25653). A magnificent plant, confined to the Kinabalu massif, and, so far as I know, not collected since the original gathering. The Kamborangah plant was fruiting, and shows setae up to 7 cm. in length, stout and very glossy.

#### TRISMEGISTIA BRAUNIANA (Bry. jav.) Fleisch.

Lumu-Lumu, Kinabalu, 1,600 m., 18 June 1925; coll. C. M. Enriquez, Herb. Singapore Bot. Gard. (18124).

New to Borneo. *Distr.* Java; Sumatra.

#### TRISMEGISTIA BRACHYPHYLLA Fleisch.

Sarawak, 1932; coll. Oxford Exped. (s.n.), c.fr.

New to Borneo. *Distr.* Sumatra.

#### TRISMEGISTIA GRACILICAULIS Dix. & Herz., sp. n.

*E gracillimis* generis. *Caules gracillimi*; ut videtur pauci cm. longi, flexuosi, parce ramosi; rami 1-2 cm. longi, iterum ramulosi. *Folia caulina* minima, vix 2 mm. longa; e basi late ovata abrupte lanceolato-loriformia, apice angustissime acutata, parce remote dentata. *Folia ramea* minora, e basi angustiore, lanceolata, sensim in acumen brevius, latius, breviter acutatum contracta, marginibus superioribus irregulariter, inaequaliter, haud spinulose dentatis. *Cellulae superiores* parvae, rhomboideae, parietibus tenuibus, marginalibus 2-3-seriebus multo longioribus, haud incrassatis, limbum bene notatum instruentibus.

*Fructus* haud visus.

*Hab.* East Borneo ; coll. Dr. Balneti, 1925 ; Herb. Herzog (2).

The extreme slenderness of the stems and the minuteness of all the parts are the leading characters ; in structure and leaf-form it is almost a miniature of *T. rigida*, but the habit is more of *T. calderensis*. The dentation of the margin is comparatively weak.

TRISMEGISTIA VALETONI Fleisch. MS. in Herb., sp. n.

E minoribus generis ; caules breves, *rigidi*, interrupte dense pinnati et bipinnati, ramis *brevibus*, 2-3 mm. longis. Folia caulina ubique distantia, *rigida*, *horride divaricata*, vix 2 mm. longa, e basi latiore ovata, subsensim in acumen latum acutum subaequilongum angustata ; ramea et ramulina multo minora, e basi angustiore sensim *lingulato-lanceolata*, breviter, late acutata ; omnia marginibus fere ubique grosse, sat aequaliter, dense spinuloso-dentatis. Cellulae laminae breves, elliptico-rhomboideae, circa  $4 \times 1$ , marginales 3-4-seriebus multo longiores, limbum sat validum bene notatum formantes.

Fructus ignotus.

*Hab.* Liang Gagang, Borneo, 1893-4, detex. Hallier ; herb. Max Fleischer, type. Moss forest, Mt. Mulu, Sarawak, 1,800-2,100 m., Nov. 1932 ; coll. Oxford Exped. (2703).

This is a very marked looking plant ; very small, very rigid, with the leaves, both moist and dry, very rigid and bristling. The leaf-form, on a reduced scale, and the areolation, however, closely resemble *T. lancifolia*, and it is possible that it is a very reduced, xerophytic form of that.

ACANTHOCLADIUM POLYMORPHUM Dix.

On ground in ' heath forest ', under 300 m., Forest Reserve, Marudi, Sarawak, Nov. 1932 ; coll. Oxford Exped. (2662 b).

New to Borneo. *Distr.* Tenasserim.

ACANTHOCLADIUM BREVIFOLIUM Dix., sp. n. (Pl. 3, fig. 31.)

Sat robustum, caespites densiusculos late extensos formans ; *nitidum*. Caules elongati, *flexuosi*, *interrupte*, *laxiuscule*, *complanate* pinnati et bipinnati, saepe *attenuati*, *subflagellacei*. Folia caulina 1.5-1.75 mm. longa, 0.5 mm. lata, e basi constricta late breviter ovato-lanceolata, *acuta nec acuminata*, concava ; margines plani vel infra anguste reflexi, e medio folio ad apicem sat conferte *subaequaliter*, *argute*, *haud grosse* dentati. Cellulae angustissime lineares, parietibus tenuibus, indistinctis, conflatis, infra parum latiores ; alares magnae, inflatae, circa trinae, intense purpureae. Folia ramea angustiora, *lingulato-lanceolata*, obtusiora, inferne obtuse, apicem versus fortiter argute denticulata. Propagula rubra, parva, subsphaerica vel ovoidea, foliorum axillis visa.

Fructus deest.

*Hab.* At base of Poch Mt., Sarawak, 1,475 m. ; coll. Everett, Herb. Mitten, ex herb. New York Bot. Gard.

Unnamed in Mitten's herbarium. Quite marked in the short, acute, but not acuminate leaves, the general habit, and the dentation, which is not coarse,

unequal, or spinulose, as is frequent in the genus, but close, short, acute, with the teeth subequal or here and there with smaller intermediate teeth.

*CLASTOBRYELLA ASPERRIMA* Dix., sp. n. (Pl. 3, fig. 34.)

*C. cuculligeræ* affinis; differt foliis *sensim multo longius, tenuius* aciculari-acuminatis, multo *fortius argutius* denticulatis, cellulis pellucidis, dorso plerumque sat conferte, *tenerrime, argute* papillois. Folia perichaetialia stricte acuminata, *dense, argute, spinuloso-denticulata*. Seta 2 cm. alta, tenuis, laevis. Theca caret. Propagula haud visa.

*Hab.* Pakka, Kinabalu, 3,100 m., 15 Nov. 1931; coll. Holttum (25646).

Very near to *C. cuculligera*, but seems constantly distinct in the narrower, longly and finely acuminate, more sharply denticulate leaves; the very finely but acutely papillose, pellucid cells, and sharply denticulate perichaetial bracts. The cells, as in some allied species, may on some of the branches be smooth or very sparsely papillose, while in *C. cuculligera* they are *at most* sparsely and lowly papillose. *C. ruficaulis* (Thw. & Mitt.) differs similarly in the leaf-form, also in the thicker seta, &c.

The absence of brood-filaments may be due to the plant gathered being a fruiting specimen.

*CLASTOBRYELLA CAPILLIFOLIA* Dix., sp. n. (Pl. 3, fig. 35.)

*C. cuculligeræ* (Bry. jav.) habitu sat similis, sed foliis laxioribus, flexuosis, *patentibus*, subfalcatis, e basi *anguste lanceolata concaviuscula* sat cito in acumen *nunc angustissime loriforme, nunc capillare, peranguste denticulatum* contractis. Cellulae *laevissimae*, alares circa trinae, magnae, vesiculosae, hyalinae. Propagula *filiformia*, articulata, hyalina, laevissima, hic illic axillis foliorum superiorum *dense aggregata* inveniuntur.

Fructus juvenis tantum visus; perichaetium parvum; bracteae foliis caulinis subsimiles, sed latiores, grossius denticulatae.

*Hab.* Stems of shrubs in shady moss forest, Dulit Ridge, Sarawak, c. 1,200 m., 13 Sept. 1932; coll. Oxford Exped. (1785 b).

A very distinct species, most nearly allied to *C. asperrima* and *C. cuculligera*, but differing at once in the form and arrangement of the leaves, which are laxly disposed, flexuose-falcate, extremely narrow at the base, and neither shortly pointed as in the latter nor gradually and longly acuminate as in the former, but rather rapidly contracted to a long capillary or loriform subula. In the above species the leaves are sharply, but not longly, and rather closely denticulate from near the base; here the basal part has the margins entire or nearly so, while the acumen is very sharply and more distantly, often almost spinulose-toothed. The cells here are entirely smooth and pellucid. The leaves may be sometimes gradually attenuated above, but more frequently are rapidly contracted above the concave base, much as is frequent in *Warburgiella*.

The brood-filaments, while in general agreeing with *Clastobryum* and *Clastobryella*, are different from any I have hitherto seen, being extremely delicate,

filiform, quite smooth, with proportionally long articulations and thin dissepiments; they are, in fact, much like the paraphyses, or vaginula hairs, of many pleurocarpous mosses, but are long, up to 0.8 mm.

*CLASTOBRYELLA RUFICAULIS* (Thw. & Mitt.) Fleisch.

Tree-trunk in rain-forest, c. 900 m., Ulu Koyan, Sarawak, 7 Nov. 1932; coll. Oxford Exped. 1932 (2531 *b*). A form with the leaves highly papillose.

New to Borneo. *Distr.* Ceylon; Malay Penins.

#### ACROPORIUM Mitt.

This interesting, but difficult genus may be said to find its centre in Borneo. Out of some sixty species (excluding the half-dozen species known from Africa and South America) at least twenty-seven occur in Borneo. Most of the species are by habit and leaf-form fairly distinct; but a few are highly variable, and these with their allies are very difficult to define. Among them may be mentioned *A. rufum*, *A. secundum*, *A. longicuspis*, and *A. aciphyllum*. The remarks under these species may help to elucidate some of the difficulties. It also has to be borne in mind that several species closely similar in leaf-form &c. are principally separated by their inflorescence.

*ACROPORIUM BOGORICUM* (Bry. jav.) Dix., comb. nov. (*Hypnum*, Bry. jav.; *Clastobryophilum* Fleisch.).

Kuala-Kurun, Borneo, 1924; coll. H. Lampmann, Herb. Herzog (23).

New to Borneo. *Distr.* Java; Sumatra; Malay Penins.

*ACROPORIUM LAEVI BOGORICUM* Dix., sp. n.

*A. bogorico* (Bry. jav.) proximum et simile; differt statura *robustiore* foliis strictioribus, cellulis *omnino laevibus*, seta etiam *ubique laevi*.

*Hab.* Rotten log in 'heath forest,' Marudi, Baram, Sarawak; in golden green cushions, 25 July 1932; coll. Oxford Exped. (1023), type. Tree-trunk in open moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 5 Oct. 1932; coll. Oxford Exped. (2135). *Ibidem*, on fallen branch in forest, 1,230–1,250 m., 18 Sept. 1932 (1930).

Possibly only a variety of *A. bogoricum*. The smooth cells alone would scarcely separate it specifically, as the papillosity varies notoriously in this genus, but the seta in *A. bogoricum* is decidedly papillose, either at the apex only or for some distance down; here it appears to be constantly quite smooth. It must, however, be admitted that no. 2135 is somewhat intermediate in some characters; with the robust habit the cells are slightly rugose and the seta is not absolutely smooth throughout, but slightly rugulose at the apex.

*ACROPORIUM SCALARE* (A. Br.) Dix., comb. nov. (*Hypnum scalare* A. Br., *Aptychella* Fleisch.).

Sibu I., Rejang River, July 1894; coll. A. H. Everett, Herb. Mitten.

New to Borneo. *Distr.* Java.

**ACROPORIUM SUBULATUM** (Hampe) Fleisch.

Upper Sarawak ; coll. Everett, Herb. Mitten.

New to Borneo. *Distr.* Philippines ; Malay Penins. ; Siam.

**ACROPORIUM PUNCTULIFERUM** (Thw. & Mitt.) Fleisch.

Baram ; N.W. Borneo ; coll. A. H. Everett, Herb. Mitten. Tree-trunks in secondary rain-forest, under 300 m., G. Dulit, Sarawak, 7 Aug. 1932 ; coll. Oxford Exped. (1145).

New to Borneo. *Distr.* Ceylon ; Malay Penins. ; New Guinea.

A feature of this species is its highly glossy leaves.

**ACROPORIUM CONVOLUTUM** (Bry. jav.) Fleisch.

Sibu, Sarawak, coll. Everett, Herb. Mitten.

**ACROPORIUM DECIPIENS** Dix.

Bettotan, near Sandakan, 25 July 1927 ; coll. C. Boden Kloss (18973 b).

**ACROPORIUM RAMULIGERUM** Dix., sp. n. (Pl. 3, fig. 39.)

Pergracile ; dense caespitosum, pallidum, flavescens, nitidum ; dense pinnatum, ramis erectis, vix 1 cm. altis, plerumque *superne attenuatis*, foliis inferioribus late patentibus, supra magis magis erectis, supremis minutis, appressis, cuspidem teretem caudiformem formantibus. Folia caulina et ramorum inferiora circa 1 mm. longa, latissime ovata, perconcava, marginibus superioribus involutis, in pilum longum subflexuosum integrum vel subintegrum raptim attenuata ; pellucida, laevia, basi cordata ; cellulae omnes breviusculae, angustae, sigmoideae, incrassatae, laevissimae, alares magnae, vesiculosae.

*Hab.* On fallen tree-trunk in white sand forest, alt. c. 1,000 m., Ulu Koyan, Sarawak, 15 Sept. 1932 ; coll. Oxford Exped. (1862). In small, rounded, shiny cushions, bright green tinged with yellow.

A very small species, almost with a Clastobryoid habit, but the leaf-form and base are quite those of *Acroporium*. The attenuated, terete, caudiform ramuli are quite distinct and are very numerous ; they do not appear to produce brood-filaments.

**ACROPORIUM RUFUM** (Hornsch. & Reinw.) Fleisch.

Above Marai-parai, Brit. N. Borneo, 1,525 m., 23 Nov. 1931 ; coll. Holttum (25117). Kamborangah, 2,200 m., 17 Nov. 1931 ; coll. Holttum (25678), a tall form with lax slender branches. Kemoel, W. Koetai, Oct. 1925 · coll. F. H. Endert (4470), Herb. Hort. Bot. Bog. (2527 c), a densely pinnate form with leaves strongly falcate-secund.

**ACROPORIUM TUBULOSUM** Broth.

Marai-parai, Brit. N. Borneo, 1,525 m., 24 Nov. 1931 ; coll. Holttum (25185). This is without fruit, but from the robust habit must be referable here rather than to *A. rufum*. The seta in the Philippines moss is smooth, which indicates a specific character of some value, though I have seen forms of *A. rufum* with



the seta scarcely papillose. Also in shady moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 20 Sept. 1932; coll. Oxford Exped. (2011). In fruit, agreeing well with the Philippines plant.

New to Borneo. *Distr.* Philippines.

*ACROPORIUM ALBIDISSIMUM* Dix.

Tree-trunk in rain-forest, c. 900 m., Ulu Koyan, Sarawak, 7 Nov. 1932; coll. Oxford Exped. (2531 c), c.fr. Fruit undescribed.

New to Borneo. *Distr.* Malay Penins.; Siam; Sumatra.

In some respects this is very near to *A. longicuspis*, and exhibits the same variability in the papillosity of the leaves. The seta here, however, is hispidulose above and much shorter; in that species it is 1.5 cm. long, and only very slightly rugulose at the apex; here it is considerably less than 1 cm. The perichaetial bracts are few, broadly ovate below, and abruptly contracted to a subulate, strict, subentire acumen.

*ACROPORIUM JOANNIS-WINKLERI* Broth.

On rotten logs and tree-trunks in open moss forest, c. 1,230 m., G. Dulit, Sarawak, 18 Sept. 1932; coll. Oxford Exped. (1933). Forming thick carpets of a yellowish green. Fruiting. This is certainly Brotherus's species, but it is a little doubtful if it be not a form of *A. longicuspis* Broth.

*ACROPORIUM RIGENS* Broth.

'Mang.', Sarawak; coll. Everett, Herb. Mitten.

Mrs. Britton suggests that 'Mang.' may refer to the habitat, and be an abbreviation for *Mangifera*. Foot of trees in dwarf forest, c. 600 m., G. Santubong, Sarawak, Dec. 1932; coll. Oxford Exped. (2723). Tree-trunk in white sand forest, c. 950 m., Ulu Koyan, Sarawak, 15 Sept. 1932; coll. Oxford Exped. (1865).

*ACROPORIUM DOWNII* (Broth.) Broth.

Tree-trunk near ground, in 'heath forest', Forest Reserve, Marudi, Sarawak, Nov. 1932; coll. Oxford Exped. (2677). Ibidem, foot of trees in dwarf forest, c. 600 m., G. Santubong, Dec. 1932 (2724). Base of tree in open moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 20 Sept. 1932; coll. Oxford Exped. (2007), a very robust form, with wider leaf-points than in the type, but connected with that by intermediate forms.

*ACROPORIUM LONGICUSPIS* Broth.

Rotten log in opening of primary forest, c. 500 m., Dulit Trail, Sarawak, 26 Aug. 1932; coll. Oxford Exped. (1514). Ibidem, c. 800 m., Ulu Koyan, 22 Sept. 1932 (2035), a form with the leaves quite smooth.

Var. nov. *ELATUM* Dix.

*Caules extensi*, usque ad 20 cm. longi, *laxifolii*. Hanging from overhanging sandstone rocks under waterfall, c. 1,230 m., Dulit Ridge, Sarawak, 12 Sept. 1932; coll. Oxford Exped. (1759); fruiting abundantly.

This is a very puzzling species, distinct enough in its ordinary forms by the narrow, not secund, longly subulate, papillose leaves; but when, as occasionally happens, all the leaves are smooth-celled, it is difficult to separate from some of the allied species. *A. Downii* may be known by the constantly falcate-secund leaves, *A. rigens* by the more crowded, longer, rigid, usually suberect leaves. *A. Joannis-Winkleri* Broth. is near it in its smooth-celled form, but is considerably more slender, with secund leaves and perichaetial bracts vaginant and abruptly cuspidate, here they are scarcely vaginant and gradually subulate.

ACROPORIUM SECUNDUM (Hornsch. & Reinw.) Fleisch. var. ANGUSTIFOLIUM Fleisch.

East Borneo; coll. Dr. Balneti, Herb. Herzog (6). An extremely small plant, which appears to me to belong here, but doubtfully. This very variable species, so common in Java and in the Malay Peninsula, appears to be rare in Borneo.

ACROPORIUM STRAMINEUM (Hornsch. & Reinw.) Fleisch.

Between Tenompok and Lumu-Lumu, 1,425–1,700 m., Brit. N. Borneo, 12 Nov. 1931; coll. Holttum (56232).

I find this and *A. turgidum* very perplexing. This plant has very turgid stems, but the branches are very obtuse, in no way cuspidate, which agrees with *A. stramineum*; but, on the other hand, the leaves are much shorter in the points than in that species, almost as short indeed as in *A. procerum*. A plant in Hooker's herbarium at Kew 'S. hyalinum, Java, Reinw.' agrees very well in habit, though less robust. This has the leaves very concave and regularly imbricated, with the appearance of *Pterobryum*. It may be an undescribed species.

Further, Kemoel, W. Koetai, Oct. 1925; coll. F. H. Endert (4536), Herb. Hort. Bot. Bog. (2512). An almost identical plant with the last. Mt. Bongoh, Sarawak; coll. Everett, Herb. Mitten, as *Sematophyllum procerum* (C. M.) Jaeg. A typical growth, though rather turgid.

ACROPORIUM MONOICUM (Lac.) Fleisch.

Kamborangah, Brit. N. Borneo, 17 Nov. 1931; coll. Holttum (K). On twig in moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 20 Sept. 1932; coll. Oxford Exped. (1998).

ACROPORIUM WARBURGII (Broth.) Fleisch. (*A. pinnatum* Fleisch.).

Base of tree in moss forest, G. Laiun, Sungei Balapau, Tinjar, Sarawak, 2 Nov. 1932; coll. Oxford Exped. (2374). A curious form, very closely and regularly pinnate, pallid in colour; leaves and cuspidate apices of branches shorter than in the type.

New to Borneo. *Distr.* Celebes; Java; Sumatra.

I can find no difference between *A. pinnatum* Fleisch. and this. Fleischer

distinguishes his species by saying that *A. Warburgii* differs in the longer stems and branches and the narrower, faintly papillose leaves. Brotherus, however, describes the cells of *A. Warburgii* as 'omnibus laevissimis'; I find the habit of the Javan plant precisely identical with those of Celebes, and I can detect no difference in the width of the leaves.

The fruit has not been described, but I have fertile specimens from Celebes, which I am describing in a paper on Celebes mosses now in preparation.

#### ACROPORIUM ACIPHYLLUM Dix.

Sibu, Sarawak; coll. Everett, Herb. Mitten. Tree in moss forest, in golden glossy tufts, c. 1,230 m., Dulit Ridge, Sarawak, 8 Oct. 1932; coll. Oxford Exped. (2188).

New to Borneo. *Distr.* Malay Penins.; Philippines.

This species in its typical form is well marked in the leaves, wide at the base, and rather rapidly narrowed to a very fine, often capillary point. It shows, however, a considerable variability, and a narrow-leaved variety from the Philippines and Malaya is very much like *A. secundum* var. *angustifolium*, but has much finer leaf-points and wider bases. The leaves may be quite straight or variously falcate.

#### ACROPORIUM DENTICULATUM Dix.

Branch of shrub in 'heath forest', under 300 m., Forest Reserve, Marudi, Sarawak, Nov. 1932; coll. Oxford Exped. (2676). A form with the leaves highly papillose.

New to Borneo. *Distr.* Malay Penins.

This well-marked species has up to now been found only in the original locality.

#### ACROPORIUM MACRO-TURGIDUM Dix., sp. n. (Pl. 4, fig. 54.)

Stirps *perrobusta*, fusco-viridis, habitu *A. turgidi* sed multo robustior. Caulis haud penduli, haud flexuosi, usque ad 10 cm. longi, ad 1 cm. lati, parce ramosi, apice breviter cuspidati, saepe curvati. Folia perconferta, plerumque, nisi apicalia horride patentia, leniter secunda, nitidiuscula, sicca saepe leniter striata, 6-7 mm. longa, 2.5 mm. lata, concaviuscula, e basi angustiore late ovata, sensim angustata, acumine leniter curvato, saepe torto, convoluto, integerrimo; ceterum eis *A. turgidi* et *A. straminei* similia, sed cellulis alaribus superne transverse divis.

Perichaetia *perbrevia*; folia arcte adpressa; e basi latissima convoluta sat cito in cuspidem breviusculam peracutam denticulatam attenuata. Seta 4 cm. longa, inferne laevis, ad apicem platytuberculata. Theca (in 2520 et 1937 tantum visa) *pendula*, turgide elliptica, deoperculata 2 mm. longa, atro-fusca.

*Hab.* G. Tahan, Pahang, Malay Penins., on ground, 1,000-1,400 m.; 28 Aug. 1928; coll. Holttum (20920), type. Kemoel, W. Koetai, Borneo, c. 1,700 m., Oct. 1925; coll. F. H. Endert (4534), Herb. Hort. Bot. Bog. (2520). On rotting logs in open moss forest, c. 1,230 m., Dulit Ridge, Sarawak, 18 Sept. 1932; coll. Oxford Exped. (1937).

The most robust (though not the tallest) species of the genus known. The leaves are much of the form of *A. turgidum* (Bry. jav.), but are widely divaricate except at the subcuspidate tips of the stems, and much larger, quite twice the dimensions given by Fleischer for *A. turgidum*. The seta also is longer, and the pendulous capsule quite distinct. A marked character is the alar cells, which are nearly always transversely divided in the upper part into two unequal cells, the lower much longer than the upper.

**ACROPORIUM PRAELONGUM** Dix., sp. n. (Pl. 3, fig. 36.)

Habitu et statura *A. proceri* (C. M.), nonnunquam paullo gracilius, aliquando simillimum. Foliorum forma, tamen, toto coelo differt, propter apicem, a basi latissima perconcava simillima, raptim in *cuspidem longiusculam acutissimam* contractum. Caules usque ad 25 cm. longi, penduli, flexuosi.

Perichaetium majusculum, turgidum, bracteis omnibus erecto-adpressis, concavis, o basi late ovata convoluta sat sensim *breviter, acutissime* acuminatis, superne argute denticulatis. Seta 2-2.5 cm. alta (in no. 2186 ad 3 cm.), laevis seu apice tantum leniter platytuberculata. Theca erecta, parva, 1.5 mm. longa, elliptica.

*Hab.* Hanging from tree-branches in moss forest, 1,250-1,300 m., Dulit Ridge, Sarawak, 4 Oct. 1932; coll. Oxford Exped. (2127), type. Ibidem, c. 1,300 m., 8 Oct. 1932 (2186).

A splendid species, in habit and size only equalled by *A. procerum*. There, however, the leaves gradually taper to a very short, broad, almost obtuse point, while here they are constricted, often very abruptly, to a long, very acute, cuspidate point, which in no. 2186 is long, flexuose, and distinctly pili-ferous. The leaf here is somewhat similar to that of my *A. aciphyllum*, but the size and habit are totally distinct. The fruiting characters also are distinct; that of *A. procerum* has not been described, but I have it from one or two localities in the Malay Peninsula. The seta there is longer, up to 4 cm., rather stouter, and the perichaetial leaves are less convolute and more widely pointed.

**MEIOTHECIUM MICROCARPUM** (Harv.) Mitt.

Branches of tree, under 300 m., Dulit Trail, Sarawak, 10 Aug. 1932; coll. Oxford Exped. (1206).

**SEMATOPHYLLUM SAPROXYLOPHILUM** (C. M.) Fleisch.

On concretionary ironstone in secondary forest, under 300 m., G. Dulit, Sarawak, 31 Aug. 1932; coll. Oxford Exped. (1581). A curious habitat for this species.

New to Borneo. *Distr.* Java; Malay Penins.; Philippines.

**WARBURGIELLA LATICUSPIS** Dix., sp. n. (Pl. 3, fig. 33.)

Dense humiliter caespitosa, sordide, pallide viridis; caulis prostratus, flexuosus, irregulariter laxe pinnatus; folia molliuscula, laxiuscule disposita, *recta, nec falcata, vix secunda*, subcomplanata, magnitudine et forma valde variabilia;

nunc 1.5 mm., nunc duplo longiora, aut breviuscule lingulato-lanceolata, haud acuminata, breviter, late, subobtusae acutae, aut longe acuminatae, latiuscule loriformia, apice fortiter denticulata; paullo concava, marginibus planis. Cellulae breviusculae, marginales saepe breviores, pellucidiores; alares magnae, circa trinae, vesiculosae, tenerae, hyalinae.

Perichaetii bracteae erectae, strictae, late breviter acutatae, dense argute denticulatae. Seta crassa, brevis, vix 5 mm. alta; theca suberecta, brevissime ovalis, castanea, deoperculata obconica; operculum rostratum; peristomium magnum, flavescens. Calyptra parva, mitriformis, ad basin laciniata.

*Hab.* Matang, Sarawak. Collector not given, but no doubt Everett; Herb. Mitten, ex herb. New York Bot. Gard.

Unnamed in Mitten's herbarium. Mitten sketches the cells as papillose, but I find them quite smooth.

Quite distinct from *W. cupressinoides* and other species in the broadly pointed leaves in no way falcate or curved.

*Warburgiella* C. M. as enlarged by Fleischer, followed by Brotherus, seems to me very hard to define. I am inclined to think it would be better to limit it (as defined by C. Müller) to species having a mitriform lacinate calyptra (as in the present plant) and suberect or erect capsules. The remaining species quite easily fall into *Sematophyllum* or *Trichosteleum*.

*Warburgiella armata* Broth. (1928) is *Mastopoma uncinifolium* (Broth.) Card.

*WARBURGIELLA NITENS* Dix., sp. n.

Gracilis; nitida, irregulariter ramosa; folia nunc stricta, nunc leniter falcata, 1.25–1.5 mm. longa, e basi lanceolata concava in acumen explicatum subulatum vel angustissime loriforme denticulatum sat raptim angustata, omnino laevia.

Perichaetium parvum, bracteis vaginula vix longioribus, e basi late ovali raptim in cuspidem longum flexuosum subpiliformem denticulatum constrictis. Seta 1 cm. longa, infra laevis, superne validiuscule papillosa. Calyptra junior solum visa, mitriformis. Fructus immaturus.

*Hab.* With *Distichophyllum cuspidatum*, on stem of shrub in shady moss forest, c. 1,300 m., Dulit Ridge, Sarawak, 17 Sept. 1932; coll. Oxford Exped. (1912).

Nearest perhaps to *W. subleptorrhynchoides* Fleisch., but with papillose seta and much narrower leaves. *W. cupressinoides* has longer smooth seta, more falcate, much less glossy leaves. *W. philippinensis* R. S. Will. differs in the gradually tapering leaves. Here, though some leaves may be found gradually tapering, they usually show the suddenly contracted subula bent at a slight angle with the concave base characteristic of *W. leptocarpa* (Schwaeg.) Fleisch. and other species.

*TRICHOSTELEUM HAMATUM* (Doz. & Molk.) Jaeg.

Borneo; Herb. Hort. Bot. Bog. (2943).

**TRICHOSTELEUM FLEXUOSO-HAMATUM** Dix., sp. n. (Pl. 4, fig. 43.)§ *Thelidium*.

Olivaceo-viride. *Sat robustum*. A *T. hamato* valde diversum foliis nec anguste convolutis nec decurvo-hamatis, sed *patentibus*, subcomplanatis, siccis madidis *flexuosis*, circa 2 mm. longis, e basi *parum concava*, latiuscule ovato-lanceolata sensim in acumen vix aequilongum *latiusculum*, fortiter denticulatum, angustata.

Fructus haud visus.

*Hab.* On wet sandstone rocks in stream-bed, c. 1,230 m., Dulit Ridge, Sarawak, 19 Sept. 1932; coll. Oxford Exped. (1975).

The habit and broad leaves seem fully to justify its separation from *T. hamatum* and the Bornean *T. palanense* (Hampe). The latter is a much smaller plant, and far nearer to *T. hamatum*.

**TRICHOSTELEUM BOSCHII** (Doz. & Molk.) Jaeg.

In numerous gatherings, and very variable; sometimes so robust as to be easily confused with *Rhaphidostichum luxurians*. The seta varies greatly in length and in degree of papillosity, and *T. brachypelma* (C. M.) is certainly only a form of this.

**TRICHOSTELEUM PSEUDO-MAMMOSUM** Fleisch.

On rotten log in open moss forest, c. 1,240 m., Dulit Ridge, Sarawak, 18 Sept. 1932; coll. Oxford Exped. (1928, p.p.). This agrees well with the description of the Javan plant, of which, however, I have been unable to see perfect specimens; the British Museum specimen of M. Fr. Arch. Ind. et Polyn. 397 is unfortunately sterile.

New to Borneo. *Distr.* Java.

**TRICHOSTELEUM EVERETTII** Dix., sp. n. (Pl. 3, fig. 40.)

Epiphyllum; *sat robustum*; caules prostrati, dense regulariter pinnati, ramis 5–8 mm. longis. Folia complanata, substricta vel leniter curvata, *haud flexuosa*, eis *T. Boschii* subsimilia sed *perbreviter*, *latiuscule* acuminata.

Folia perichaetialia longa, stricta, grosse denticulata, dorso *alte*, *argute* papillosa. Seta *longa*, usque ad 2 cm. alta, tenuis, flexuosa, ad summam apicem rugoso-papillosa. Theca perminuta, erecta, sicca macrostoma.

*Hab.* Base of Bongoh Mt., Sarawak; coll. Everett, Herb. Mitten, ex Herb. New York Bot. Gard., type. Borneo, Sept. 1892; coll. A. H. Everett (678).

Of the affinity of *T. Boschii*, but much more robust, with short and often wide, not flexuose leaf-points, much longer seta, and erect or suberect capsule. *T. longisetulum* Fleisch. has a seta almost as long, but smooth above, the capsule inclined or pendulous. A rather unusual feature is found in the perichaetial leaves. Usually in species with papillose leaves, the former are less strongly papillose or smooth; here they are more highly and acutely papillose than the stem-leaves, which are quite strongly so.

*TRICHOSTELEUM PROCERUM* Dix., sp. n. (Pl. 4, fig. 45.)

*E. robustissimis* generis. Caespites *late extensi*, straminei; caules ad 8 cm. longi, prostrati, radiculosi, flexuosi, robusti, interrupte pinnati, ramis 1-2 cm. longi, parce ramosi, obtusi, *subcomplanati*, 2 mm. lati. Folia sat conferta, 1.5 mm. longa, 0.5 mm. lata, e basi angustiore, vix constricta, *latissime ovata*, cito in *cuspidem curvatam acutam*, integram contracta, parum concava. Cellulae lineares, pellucidae, leniter papillosae vel laeves; alares utrinque 3-4, magnae, vesiculosae; supra-ales *plures, majusculae, hyalinae*. Folia ramea *perconcava*, minora, brevius, minus acute cuspidata, cellulis dorso *alte, acute, conspicue* papillosis. Perichaetia *longa*, bractae erectae, e basi longe convoluta sat cito in subulam *validam, loriformem, sparse argute denticulatam* contracta. Seta *praelonga*, 3-4 cm. alta, flexuosa, laevis. Theca *cernua, turgide ovata, gibbosa*, operculum longirostratum, thecam aequans vel superans.

*Hab.* Labuan, Borneo; coll. Motley (18), Herb. Mitten, ex herb. New York Bot. Gard., type. Sandy banks in clearing, Marudi, Baram, Sarawak, 25 July 1932; coll. Oxford Exped. (1018).

Var. *LAEVIFOLIUM* Dix.

Folia omnino vel fere omnino *laevia*.

*Hab.* In a wet grassy marsh near the town of Bruné, Borneo; 1852; coll. Motley (10), Herb. Mitten, ex herb. New York Bot. Gard.

Unnamed in Mitten's herbarium.

Perhaps the largest species known of the genus; terrestrial and probably more or less hygrophytic. The very broad leaves, wide above and then abruptly acutely cuspidate, the cuspidate point curved or twisted, the entire or subentire margins, and the marked fruiting characters are very distinct. The Bruné plant has the branch leaves quite smooth, and I took it to be a distinct species. Further examination, however, showed it to be identical except in this respect with the Labuan plant. The basal areolation is rather marked in having several supra-alar cells large and hyaline. The Marudi plant is sterile, more rigid, more densely pinnate, with shorter branches.

*TRICHOSTELEUM INFLEXIFOLIUM* Dix., sp. n. (Pl. 4, fig. 44.)

Gracilescens; *molle*; *palescens*, nitidum; habitus potius *Ectropothecii*, tanquam *E. falciformis*. Caules *extensi*, *distanter, irregulariter, complanate pinnati*; ramis tenellis, flexuosis, vix 5 mm. longis. Folia *laxe disposita*, imbricatula, patula, sicca *apicibus inflexis*; circa 1 mm. longa, mollia, *perconcava*, e basi angusta *late cochleari-ovata, brevissime late acutata, perpellucida*; cellulae breviusculae, incrassatae, sed parietibus tenerrimis subconflatis, unde areolatio valde pellucida; papillae *tuberculosae praealtae pernotatae*.

Bractae perichaetii erectae, concavae, papillosae, sensim vel abrupte in acumen latiusculum fortiter denticulatum angustatae, apud basin acuminis saepe laceratae. Seta 1.5 cm. longa, infra laevis, dimidia parte superiore papillosa, apice papillis densis grossis praedita. Theca inclinata, oblonga, collo distincto, annulato; operculum aequilongum, aciculare.

*Hab.* On rotting fallen branch in shady moss forest, alt. c. 1,300 m., Dulit Ridge, Sarawak, 17 Sept. 1932; coll. Oxford Exped. (1911).

A very distinct species, both in habit and texture, and in the cochleariform, scarcely pointed leaves, pellucid and highly papillose. The leaves when dry are little altered, and with the inflexed apex, somewhat divaricate base, and lax disposition give a very distinct appearance to the branches. The stem- and branch-leaves are very similar to one another.

TRICHOSTELEUM LEPTOCARPUM (Schwaegr.) Fleisch.

Sarawak, coll. Everett, Herb. Mitt.

Var. nov. ALTEPAPILLOSUM Dix. Cellulae *alte, fortiter papillosae*.

Tenompok, Brit. N. Borneo, 1,525 m. 1931-2; coll. J. & M. S. Clemens, Herb. Hort. Bot. Bog. (2974). A distinct variety.

RHAPHIDOSTICHUM MALAYANUM (Dix.) Dix., comb. nov.

An einem Baumstamm, Tandjoeng Redet, Bez Beran, East Borneo, 1913; coll. Wegner, Herb. Herzog.

New to Borneo. *Distr.* Malay Penins.

Not collected, I believe, since the original gathering. Brotherus places this in *Warburgiella*, but I prefer to put it with *R. pycnophyllum* (C. M.) in the present genus.

RHAPHIDOSTICHUM SURCULARE (Dix.) Dix., comb. nov.

On twigs, Kinabalu, 1932; coll. J. & M. S. Clemens, Herb. Hort. Bot. Bog. (2969 a). Base of small tree in primary forest, c. 400 m., Dulit Trail, Sarawak, 30 Sept. 1932; coll. Oxford Exped. (2092).

New to Borneo. *Distr.* Malay Penins.; Ceylon.

The fruit of this has not been found, but the microphyllous ramuli are very pronounced; in 2969 a they are very numerous and about 2 cm. long! The Ceylon plant was labelled as 'C. M. 243, ? *Sematophyllum asperifolium* Thw. & Mitt.', but I do not know whether it was distributed by Thwaites.

RHAPHIDOSTICHUM RAMULINUM (Thw. & Mitt.) Broth.

Bongaya, Borneo, Dec. 1897; coll. Ridley (468). Shrubs in 'heath forest', c. 800 m., Ulu Koyan, Sarawak, 25 Sept. 1932; coll. Oxford Exped. (2069, 2071 b). Base of Bongoh Mt., Sarawak; coll. Everett, Herb. Mitten.

New to Borneo. *Distr.* Ceylon.

RHAPHIDOSTICHUM AQUATICUM Dix., sp. n. (Pl. 3, fig. 38.)

Sat robustum, sordide viride, submolle, *aquaticum*, habitu fornicis robustioribus *Ectropotheccii Zollingeri*; rami 1-1.5 cm. longi, *subcomplanati*, leniter curvati, *laxiuscule* foliosi. Folia 1-1.25 mm. longa, 0.4-0.5 mm. lata, vel paullo ultra, e basi constricta *late oblongo-ovata*, *apice brevissime late angustato*, *saepe sub-obtus*o, perconcava, sub apice saepe leniter constricta; margines parte superiore indistincte denticulati. Cellulae anguste lineares, *peropacae*, parietibus



tenuibus indistinctis, dorso *grosse*, sat *humiliter ruguloso-papillosae*; alares utroque latere *plures, vesiculosae, a margine sensim decrescentes*. Folia perichaetialia e basi ovata, haud convoluta, *raptim* in subulam *subaequilongam loriformem* argute denticulatam contracta. Seta circa 1 cm. alta, laevis, ad apicem tantum leniter rugulosa. Theca (in 2173) minuta, *erecta vel suberecta*, castanea, e collo defluente turgide ovata, sicca urceolata; operculum aciculari-rostratum, thecam aequans.

*Hab.* G. Matang, Sarawak, c. 150 m., submerged on rock in small stream, 22 Jan. 1930; coll. Holttum (23165), type. Sandstone boulders in torrent, 300–500 m., G. Dulit, Sarawak, Oct.–Nov. 1932; coll. Oxford Exped. (2273, 2619).

An aquatic species, distinct in habit and in the very short broad points of the leaves; these vary somewhat in length and acuteness, are sometimes distinctly constricted below the apex in the way characteristic of the genus, at other times not at all. The cells are very opaque from the cell-contents, and the walls being more or less concolorous or paler are indistinct; the dorsal papillae are coarse, but not very high, sometimes rather rugulosity than papillae. The leaves are not unlike those of *R. Bruckii*, but smaller, with broader and shorter points, and the leaf-arrangement quite different.

*RHAPHIDOSTICHUM DUBIUM* Dix., sp. n. (Pl. 4, fig. 42.)

Sat robustum; flavesces, parum nitidum; caules *dense* pinnati, ramis erectis, 6–7 mm. longis, *siccis leniter curvatis, breviter cuspidatis, turgidis*. Folia conferta, plus minusve secunda, 2 mm. longa, caulina ovata, sensim, breviter loriformia, inferne concava, marginibus involutis, inde *acumine concavo marginibus late explicatis*, subdenticulatis; cellulae sublaeves, alares Sematophylloideae, magnae, aurantiacae. Folia ramea multo brevius, latius acuminata, apud basin acuminis *constricta*, marginibus fortius denticulatis, cellulis *breviusculis, parietibus incrassatis, porosis*, lumine *papilla unica grossiuscula* munito.

Fructus ignotus.

*Hab.* Sarawak, 1932; coll. Oxford Exped. (2707).

This plant has the habit of *Acroporium*, but the leaf-form and structure of *Trichosteleum* or *Rhaphidostichum*. Its position is rather uncertain, but the leaves have a closer resemblance to *Rhaphidostichum* than to *Trichosteleum*, both in the leaf-base and in the acumen. The habit is somewhat that of a short *Acroporium secundum* or *hermaphroditum*.

*ACANTHORRHYNCHIUM PAPILLATUM* (Harv.) Fleisch.

In several gatherings, and exceedingly variable in size, form of leaf, and length of subula. Some of the forms would seem well worth a varietal name, but are connected with the type by intermediates and are therefore difficult to define,

*ACANTHORRHYNCHIUM SUBINTEGRUM* (Broth. & Dix.) Broth.

By small stream in swampy forest, under 300 m., Forest Reserve, Marudi, Sarawak, Nov. 1932; coll. Oxford Exped. (2664).

Brotherus is certainly right in referring it to this genus.

*TAXITHELIELLA* Dix., gen. nov. Sematophyllacearum.

Habitu *Taxithelii*, sed dense, late extensa. Folia late ovalia, breviter acuta; areolatio laxa, cellulae late rhomboideae, quaeque dorso papillis circa 3–4 magnis sed humilibus, saepe transverse elongatis, praedita.

Autoica. Seta brevis; theca minuta, erecta, symmetrica, leptodermica, acetate macrostoma; exothecii rete laxum, e cellulis hexagonis, pellucidis, parietibus tenuibus, saepe curvatis, vix collenchymaticis instructum. Operculum longirostre. Calyptra parvum, nudum. Peristomium pallidum, dentes ad basin cohaerentes, haud vel tenerrime et indistincte striolati, superne sparse et tenerrime papilloso. Endostomii membrana nulla; processus subrobuste filiformes, fusci, dentibus aequilongi, fortiter lamellati, inter lamellas angustissime rimosi, lamellis intus fortiter prominentibus. Spori parvi.

*TAXITHELIELLA RICHARDSONII* Dix., sp. n. (Pl. 4, fig. 47.)

Stirps pulcher, caespites latos, depressos, densos, glauco-virides, haud nitentes, formans. Caules breves, repentes, molles, fragiles, laxe subcomplanate ramosi, ramis hic illic ramulosis. Folia laxiuscula, complanata, subhorizontaliter subcomplanate patentia, quinquefaria, e basi angustiore late ovata, brevissime, late acuta, marginibus planis, integerrimis; ecostata; cellulae pellucidae, late rhomboideae vel fusiformes, 10–13  $\mu$  latae, nunc elongatae, nunc perbreves (25–30  $\mu$  longae) versus apicem breviores ( $1\frac{1}{2} \times 1$ ), parietibus tenuibus, pellucidis. Papillae limitibus longitudinalibus sitae, etiam in medio lumine, seriatas, magnas, conicas, altiusculas. Cellulae alares paucae, subquadratae, pellucidae.

Flores ♂ prope femineos. Perichaetia parva, paucifolia, bractae pellucidae, vix vaginam superantes, lanceolatae, irregulariter denticulatae, internae saepe laciniatae. Seta circa 4 mm., debilis. Fructus character supra descriptus.

*Hab.* Rotten logs and lianes in forest undergrowth on ridge, under 300 m., G. Dulit, Sarawak, in vivid green patches or carpets, 16 Aug. 1932; coll. Oxford Exped. (1323).

A remarkable little plant. The fruit and peristome might place it in Fabroniaceae, e.g. near *Anacamptodon*; the peristome, however, is similar to e.g. *Rhizohypnella* in the Hylocomiaceae; while the size and seriately papillose cells strongly support the affinity with *Taxithelium*.

The papillae are peculiar. They are situated in the middle of the cell lumen, but also on the longitudinal walls. As far as I have been able to make out, the protuberances on the dividing walls are on the same level as the median ones, and are probably extended laterally across the cell towards each papilla, possibly uniting with it; in any case the appearance is frequently given of

transversely elongate papillae, so that under low powers, in certain illuminations, they appear as lines across the cells, which therefore take on a rather striking Sphagnoid look.

**TAXITHELIUM GOTTSCHAEANUM** (Hampe) Broth. (*T. subtrachaelophyllum* Dix.).

Base of Bongoh Mt., Sarawak; coll. Everett, Herb. Mitten. Twigs and leaves of shrubs, in damp rocky rain-forest, under 300 m., Dulit Trail, Sarawak, 19 Aug. 1932; coll. Oxford Exped. (1180). Ibidem, shrub in spray of waterfall, c. 500 m., 17 Nov. 1932 (2616).

This species is probably best distinguished from *T. nepalense* by the capsules practically erect and symmetric, wide-mouthed when dry, rather than by any structural characters in the leaves, which, however, are much larger, more laxly arranged, more horizontally spreading, and more glossy than in *T. nepalense*. I think that my *T. subtrachaelophyllum* can hardly be separated from *T. Gottscheanum*.

**TAXITHELIUM KERIANUM** (Broth.) Broth. (*T. horridulum* Broth.).

Koela-Koeroen, Borneo, 1927; coll. H. Lampmann, Herb. Herzog. Below Dallas, Brit. N. Borneo, c. 1,000 m., 6 Nov. 1931; coll. Holttum (25280 b).

This is, I believe, a much more widely distributed species than has generally been recognized. *T. horridulum* Broth., from the Philippines, certainly belongs here, from original specimens.

**TAXITHELIUM WERNERI** (Herz.) Broth. (*T. epiphyllum* Broth.).

Epiphyllous on various plants in primary forest, under 300 m., S. Balapau, Ulu Tinjar, Sarawak, 1 Nov. 1932; coll. Oxford Exped. (2454).

New to Borneo. *Distr.* New Guinea.

The Bornean *T. epiphyllum*, from original specimens, certainly belongs to this species.

**TAXITHELIUM ISOCADIODES** Dix.

Tenompok, Brit. N. Borneo, 1,425 m., 11 Nov. 1931; coll. Holttum (25327).

New to Borneo. *Distr.* Malay Penins.

**TAXITHELIUM CONVOLUTUM** Dix., sp. n. (Pl. 3, fig. 41.)

Gracile. Epiphyllum, caulibus prostratis, elongatis, aequaliter, brevissime, dense pinnatis, ramis tantum 3–4 mm. longis, complanatis, obtusis. Folia parva, vix 1 mm. longa, subhorizontaliter divergentia, lanceolata, perconcava, supra convoluta, breviter, stricte, haud tenuiter acutata; margines superiores ob papillas altas exstantes quasi tenui-denticulati. Cellulae angustissime lineares, pluri-papillatae; papillae tenues sed altae, spinulosae. Cellulae alares et supra-alares numerosae, subquadratae, laxae, hyalinae, sed haud vesiculosae.

Autoicum. Perichaetium laxifolium, foliis e basi late ovali sensim vel raptim in acumen longe loriforme vel subulatum flexuosum, subrecurvum, denticulatum angustatis, Seta usque ad 2 cm. longa, tenuissima; theca

*minuta*, erecta vel suberecta, sicca macrostoma, atro-fusca; operculum conico-rostellatum.

*Hab.* Upper Sarawak; coll. Everett; Herb. Mitten, type. On leaf, Sibul, Sarawak; coll. Everett, Herb. Mitten. On leaf of palm in undergrowth of forest by torrent, under 300 m., G. Dulit, Sarawak, 12 Nov. 1932; coll. Oxford Exped. (2563).

Of the group to which *T. kerianum*, *T. Werneri*, &c., belong, but distinct in the slender habit, very short, equally pinnate branching, and the strict, shortly pointed, convolute leaves. *T. kerianum* has similarly formed leaves, but they are without the papillate-denticulate leaf-margins, the plant is more robust, with different branching, and the seta much shorter.

**TAXITHELIUM LINDBERGHII** (Bry. jav.) Ren. & Card.

Kamborangah, Brit. N. Borneo, 2,200 m., 17 Nov. 1931; coll. Holttum (25681 b). A soft, elongate, pendulous plant, with the habit of a delicate *Barbella*; the leaf-form agrees well, and the papillae, though often wanting, are sometimes quite distinct. I am uncertain whether it belongs here or should be made a new species.

**TAXITHELIUM SUMATRANUM** (Bry. jav.) Broth.

Base of Bongoh Mt., Sarawak; coll. Everett, Herb. Mitten.

New to Borneo. *Distr.* Sumatra.

**TAXITHELIUM DISTICHOPHYLLUM** (Hampe) Broth.

Sarawak; coll. Everett; and Borneo; coll. Everett; Herb. Mitten. Dry limestone rock in cave, under 300 m., Bidi, Ulu Sarawak, Dec. 1932; coll. Oxford Exped. (2752).

New to Borneo. *Distr.* New Guinea; Java; Amboina; Celebes; Philippines; Siam.

**TAXITHELIUM MAGNUM** Fleisch.

Kemoel, W. Koetai, Sept. 1925; coll. F. H. Endert (3676 a), Herb. Hort. Bot. Bog. (2523).

New to Borneo. *Distr.* Sumatra; Java; Malay Penins.

**TAXITHELIUM BILOBATUM** Dix.

Sandstone rocks in bed of stream, G. Dulit, Sarawak, 5 Aug. 1932; coll. Oxford Exped. (1131). In dark green patches.

New to Borneo. *Distr.* Malay Penins.; Assam.

**TAXITHELIUM MICRO-SIMILANS** Dix., sp. n. (Pl. 4, fig. 46.)

*T. similanti* (Bry. jav.) peraffine; differt autem *statura minore*, foliis circa 0.75 mm. longa (nec 1.5 mm.), rameis haud rotundato-obtusis, sed late breviter apiculatis vel obtuso-acutis.

*Hab.* Pak Munung, Wieng chan, Laos, on trees in light evergreen forest, c. 1,400 m., 23 Apr. 1932; coll. A. F. Kerr (526 g), type. Tenompok, Brit.

N. Borneo, 1,525 m., 1931-2; coll. J. & M. S. Clemens, Herb. Hort. Bot. Bog. (2970 b).

Very near to *T. similans*, but considerably smaller, with leaves only half the size, and with the leaf-apex always more or less pointed or apiculate. In *T. similans* they are sometimes truncate, but usually, the branch-leaves, at least, broadly rounded and obtuse.

The stem-leaves and branch-leaves here appear to be more differentiated than in *T. similans*; the stem-leaves have a rather narrow, shortly and widely pointed apex, and are almost or quite smooth; the branch-leaves are wider above, abruptly narrowed and with a short blunt apiculus; and the cells are markedly spiculose at the back.

There appears to me a good deal to be said for separating the subgenus *Anastigma* Card. generically from *Taxithelium*. But I cannot think the genus *Glossadelphus* as defined by Fleischer, and followed by Brotherus, is at all a natural one. The group containing *G. Zollingeri*, e.g., appears to me far removed from the *Anastigma* group, and much more closely related to *Ectropothecium*, and I should retain all the species placed by Brotherus (Musci, ed. ii. p. 444) under the group A of *Anastigma*, in that genus, including all the rest in *Glossadelphus*—excepting *T. isopterygioides* Dix., which belongs to A. How elusive the distinctions are in the genus as extended by Fleischer may be seen from the fact that two or three of the species in A appear in the 'Musci' under more than one genus, viz. *Isopterygium* and *Taxiphyllum*, as well as *Glossadelphus*!

#### MYURIACEAE.

MYURIUM PURPURATUM (Mitt.) Broth.

On tree-trunk in white sand forest, c. 1,000 m., 15 Sept. 1932; coll. Oxford Exped. (1860).

New to Borneo. *Distr.* New Hebrides; New Caledonia; Fiji. An interesting extension of the range of this beautiful species.

PILOECIUM PSEUDO-RUFESCENS (Hampe) C. M.

Tree-trunk, under 300 m., G. Dulit, Sarawak, 19 Oct. 1932; coll. Oxford Exped. (2198).

PILOECIUM ACROPOROIDES Dix., sp. n. (Pl. 3, fig. 37.)

Habitu *P. pseudo-rufescentis* sed minus. Folia minora, breviora, sicca suberecta, vix patentia, unde caulis multo angustior, gracilior. Stramineo-flavum, nitidum, 1-1.5 cm. altum. Folia tantum 2-2.25 mm. longa (*P. pseudo-rufescente* 4 mm. vel ultra), versus apicem leniter tantum denticulata, saepe subintegra. Cellulae superiores breviores, angustiores; alares omnino Sematophylloideae, haud scalariformes, circa trinae externae magnae, vesiculosae, hyalinae, internae angustae, aurantiacae. Fructus ei *P. pseudo-rufescentis* subsimilis. Exothecii cellulae ad angulos fortiter collenchymaticae.

Tree-trunk, near 'ground, in 'heath forest,' under 300 m., Forest Reserve, Marudi, Sarawak, Nov. 1932; coll. Oxford Exped. (2672).

At first sight this resembles a small form of *P. pseudo-rufescens*, but structurally is very distinct; the leaves are much smaller, less denticulate, with much shorter and smaller upper cells, and the alar cells are entirely different. In the earlier species they are thick-walled and scalariform, in several series vertically and laterally, which, with the plicate leaves led Fleischer to place the genus near to *Myurium*. The alar cells in the present species are incontrovertibly Sematophylloid, and in my opinion, while quite agreeing that the genus should be placed in the Myuriaceae, the true position of that family should be near Sematophyllaceae.

### HYPNACEAE.

*ECTROPOTHECIUM PENZIGIANUM* Fleisch. var. *RIGENS* Fleisch.

Silau Basin, Kinabalu, 1931-2; coll. J. & M. S. Clemens, Herb. Hort. Bot. Bog. (2968).

Species new to Borneo. *Distr.* Java; Celebes.

*ECTROPOTHECIUM BUITENZORGII* (Bél.) Jaeg.

Tenompok, 1,425 m., Brit. N. Borneo; 10 Nov. 1931; coll. Holttum (25324).

New to Borneo. *Distr.* Wide.

*ECTROPOTHECIUM SUBLATICUSPIS* Dix., sp. n. (Pl. 4, fig. 48.)

Dioicum. *E. laticuspidi* Broth. Novae Guineae affine et simile. Differt foliis magis regulariter et fortiter falcatis, marginibusque *integr*is. Ab *E. borneënsi* Broth. & Geh. differt foliis *falcato-decurvis*, *marginibus integr*is, cellulis multo *angustioribus*.

*Hab.* Maraiparai, Brit. N. Borneo, 1,525 m., 24 Nov. 1931; coll. Holttum (25183).

This species resembles *E. laticuspis* and *E. borneënsis* in the habit and the form of the broad, short, very shortly and widely pointed leaves; it differs at once, however, from both in the leaves, both of stem and branches, being quite entire. No fruit was present.

*ECTROPOTHECIUM ERYTHROCAULE* Dix., sp. n.

Dioicum. *E. Moritzii* habitu fere simile, sed gracilius. *Epiphyllum*. Caules elongati, 10 cm. longi et ultra; inter ramos superficie dorsali *saepe pulchre rubri*; pectinatim pinnati, ramis subaequalibus, circa 4 mm. longis, nitidis. Folia falcato-decurva, caulina e basi *late cordato-auriculata* sensim in acumen angustum acutum *longiusculum* dentatum attenuata. Folia ramea minora, e basi multo angustiore ovata, *breviter*, latius acuminata, versus apicem argute denticulata; omnia textura *perpellucida, tenerrima*, e cellulis *angustissimis*, 3-4  $\mu$  tantum latis, marginalibus *haud diversis*, basilaribus haud vel vix latioribus instructa. Cellulae alares vix ullae.

Fructus ignotus.

*Hab.* On leaves of shrub in 'heath forest', c. 800 m., Ulu Koyan, Sarawak, 25 Sept. 1932; coll. Oxford Exped. (2071).

Although sterile, and although very similar to *E. Moritzii* in habit and in the acutely, closely toothed branch-leaves, it is a quite different plant. The leaves are of an excessively thin pellucid areolation, all the cells being very long and narrow, the marginal not differentiated as in *E. Moritzii* and *E. cyperoides*, the basal and alar scarcely enlarged—though two or three lax, hyaline, vesicular alar cells may sometimes be detached from the stem with the leaf. The broadly cordate auriculate leaf-base of the stem-leaves is a marked character. The red colour of the upper surface of the stem (not due to radicles) is very pretty, but may not be a constant specific character.

*ECTROPOTHECIUM TURGIDUM* Dix., sp. n. (Pl. 4, fig. 49.)

Dioicum videtur; flores ♂ haud visi. Robustum, *densissime compactum*, ochraceo-viride, caespites *tumescens* formans. Caulis breviusculus, *perconfer*te ramosus, ramis suberectis 5–10 mm. longis, *obtusis, turgidis*. Folia sicca madida *rigide patula*, subsecunda, *haud falcata*; caulina 2 mm. longa, vel paullo ultra, e basi sat anguste cordata ovato-lanceolata, sensim angustata, inde cito stricte argute longiter acuminata, concaviuscula, superne leniter *rugosa*, marginibus planis, e basi fere denticulatis, prope apicem argute, infra minute. Costa bina, *brevis, bene notata*. Cellulae angustissimae, ad folii basin breviores, latiores, incrassatae, valde porosae; alares plures, majusculae, inanes, subquadratae. Folia ramea breviora, breviter acuta, fortius denticulata, perconcava, sicca *striatula vel rugulosa, nitida*.

Perichaetia sat magna; folia caulinis similia, sed basi latiore, subconvoluta, acumine patente, subflexuoso, argute denticulato. Seta 3 cm. longa, vel paullo ultra; theca *magna*, deoperculata 2–2.25 mm. longa, e collo distincto curvato turgide elliptica, castanea, rugulosa, pendula. Operculum conicum, alte apiculatum. Calyptra haud visa.

*Hab.* Pakka, Kinabalu, alt. 3100 m., 15 Nov. 1931; coll. Holttum (25650). The stems in this species are not elongate, but very densely tufted, and closely branched, forming turgid cushions. The leaves are not or hardly falcate, sharply toothed above, with very narrow areolation, not differentiated at margin. The habit, leaf-form, distinct though short nerves, rugosity, and sharp toothing of leaves suggest *Gollania*, but the pendulous capsule indicates *Ectropothecium*.

*ECTROPOTHECIUM INTORQUATUM* (Doz. & Molk.) Jaeg.

Tenompok, Brit. N. Borneo, c. 1,425 m., 10 Nov. 1931; coll. Holttum (25332). Ibidem, 11 Nov. 1931 (25348), epiphyllous. Kamborangah, 2,200 m., 17 Nov. 1931; coll. Holttum (25679, 25681).

New to Borneo. *Distr.* Java; Sumatra; Celebes; Ceram; Ternate; Halmahera; Philippines.

*ECTROPOTHECIUM BORNEËNSE* Broth. & Geh.

Stream below Dallas, Brit. N. Borneo, 760 m., 9 Nov. 1931; coll. Holttum (25372). S. Blooe, 1896–7; coll. Jaheri (1121), Herb. Hort. Bot. Bog. (2018).

*ECTROPOTHECIUM ICHNOTOCLADUM* (C. M.) Jaeg.

Sibu, Sarawak ; coll. Everett, Herb. Mitten. Lobang, North Borneo, c. 1,225 m., 19 Nov. 1931 ; coll. Holttum (25339).

*ECTROPOTHECIUM MORITZII* (C. M.) Jaeg.

Kiau, W. Koetai, Oct. 1925 ; coll. F. H. Endert (4697), Herb. Hort. Bot. Bog. (2549). Rotten trunk in primary forest, under 300 m., G. Dulit, Sarawak, 22 Aug. 1932 ; coll. Oxford Exped. (1424). Ibidem, on rotten log by stream, 2 Sept. 1932 (1608). These two numbers represent a remarkable form, having the perichaetia frequently synoicous, and the bracts sometimes few, abruptly contracted to a fine subula. These characters, however, prove to be inconstant, and it is best considered a forma heteroica.

*ECTROPOTHECIUM INCUBANS* (Hornsch. & Reinw.) var. *SCABERULUM* (Broth.) Fleisch.

Sibu, Sarawak ; coll. Everett, Herb. Mitten. Baram, Sept. 1892 ; coll. Everett, Herb. Mitten.

*ECTROPOTHECIUM VERRUCOSUM* (Hampe) Jaeg.

Lobang, Brit. N. Borneo, c. 1,225 m., 19 Nov. 1931 ; coll. Holttum (25339 b).

*ECTROPOTHECIUM DENTATUM* Dix., sp. n. (Pl. 4, fig. 50.)

Diicum. Sat robustum, sordide viride, *molle*, late extensum ; caules prostrati, *flexuosi*, irregulariter, complanate ramosi, vix nitidi. *Paraphyllia* sparsa caulibus inveniuntur. Folia caulina *sat laxa*, circa 1.5 mm. longa, *complanata*, *leniter falcata*, *mollia*, e basi latiore sensim in acumen angustum *breviusculum denticulatum* attenuata. Costa bina, brevis, male definita. Cellulae perangustae, conflatae, pellucidae, versus basin paullo latiores, infimae circa 2-seriebus *laxae*, *hyalinae*. Alares nullae. Folia ramea *percomplanata*, haud falcata, *concava*, marginibus saepe, praecipue prope apicem, anguste involutis, *fortiter denticulatis*.

Perichaetia stricta, bracteae *erectae*, sensim longe subpiliformiter acuminatae, fortiter denticulatae. Seta circa 2 cm. alta, *infra crassa*, *superne valde attenuata*. Theca sat parva, elongata, pendula ; operculum e basi hemisphaerica aciculari-rostellatum. Flores ♂ caulibus propriis copiosi geruntur.

*Hab.* Sarawak, coll. A. H. Everett, Herb. Mitten, ex herb. New York Bot. Gard., type. Below Dallas, Brit. N. Borneo, c. 900 m., 6 Nov. 1931 ; coll. Holttum (25676).

Mitten's plant was labelled *Ectropothecium bornense* Mitt. MS. in herb., but the name is preoccupied by Brotherus and Geheeb's species.

The characters are not very distinctive, but the soft lax habit, very complanate branching and foliation, and non-falcate leaves separate it from all its allies. *E. percomplanatum* Broth. in many ways resembles it, but is in all respects a much smaller plant.



*VESICULARIA MIQUELII* (C. M.) Fleisch.

In numerous gatherings.

*ISOPTERYGIUM TEXTORI* (Lac.) Mitt.

Dry sandstone ledge under waterfall, c. 1,230 m., Dulit Ridge, Sarawak, Sept. 1932; coll. Oxford Exped. (2048).

It is no doubt by a slip that Brotherus omits Borneo from the distribution of this species. It is much wider than as given by him; I have it in my herbarium in addition from China, Formosa, South India, and Malay Peninsula.

*ISOPTERYGIUM GRACILISETUM* (Hornsch. & Reinw.) Jaeg.

Base of Bongoh Mt., Sarawak; coll. Everett, Herb. Mitten. On leaf, Sarawak; coll. A. H. Everett, Herb. Mitten. Foot of G. Damoes, 1893-4; coll. Hallier (4149), Herb. Hort. Bot. Bog. (2017).

*ISOPTERYGIUM FISSUM* Dix., sp. n.

Habitu *I. albescentis*, sed multo robustius, subnitidum. Caules elongati, prostrati, sat regulariter pinnati, ramis complanatis, circa 6 mm. longis. Folia patentia, 1.5-1.75 mm. longa, 0.35-0.5 mm. lata, e basi angustiore haud constricta ovato-lanceolata, caulina breviter anguste acuminata, ramea late acuta, viz acuminata, infra uno latere inflexo, supra integra; ecostati; cellulæ anguste lineares, pellucidae, infra paullo laxiores, ad infimam basin circa 2-seriatae laxiores, hyalinae, alares ab illis vix diversae.

Autoicum. Perichaetium magnum, polyphyllum, bracteis e basi late ovali sensim longe, substriate, haud tenuiter acuminatae, subintegrae, internae ad acuminis basin fortiter profunde laciniatae. Seta 2 cm. alta, vel paullo ultra. Theca cernua vel pendula, saepius curvata, brevis; operculum rostellatum.

*Hab.* Sandakan, Myburgh Prov., Borneo, Oct.-Dec. 1921; coll. A. D. E. Elmer (20366).

In habit and leaf-form not unlike *I. bancanum*, but pale in colour, with entire leaves and longer seta; *I. albens* has much smaller and much more narrowly attenuate leaves; *I. gracilisetum* also has the leaves more narrowly acuminate and denticulate; while from all it differs in the strongly lacinate inner perichaetial bracts.

*ISOPTERYGIUM BATTAKENSE* Fleisch.

Wet rocks in shade, in primary forest, c. 700 m., Dulit Trail, Sarawak, 27 Aug. 1932; coll. Oxford Exped. (1503a).

This agrees well with Fleischer's type, which I have examined by the kindness of the Curator of the Farlow Herbarium.

New to Borneo. *Distr.* Sumatra.

#### DIPHYSCIACEAE.

*DIPHYSCIUM RHYNCHOPHORUM* Dix., sp. n. (Pl. 4, fig. 53.)

*D. fasciculato* Mitt. affine. Elatum, laxè, late aggregatum, 3-4 cm. altum, robustum, atro-fuscum. Folia conferta, inferiora parva, apicalia comosa,

siccitate rigide incurvo-flexuosa, 6–7 mm. longa, e basi brevi, dilatata, ovata, concava, aurantiaca, in laminam supra basin paullo angustiore linguatam angustata. Apex folii nunc subobtusus nunc acutus, *subito in cuspidem proboscoideum robustum strictum vel curvatum prolongatus*. Costa ad basin latissima, superne angustata, in cuspidem peranguste percurrent. Folii margines a media lamina *grosse, irregulariter, inaequaliter runcinato-dentati*. Cellulae obscurae, isodiametricae, irregulares, parietibus subincrassatis, subpellucidis, media lamina *bistratosae*, versus marginem 3–4-stratosae, *limbum crassum*, aetate *fuscum* instrucentes.

Folia perichaetialia minus dentata, sensim acuminata, in aristam validam integram longam producta. Fructus haud visus.

*Hab.* On submerged sandstone rocks in bed of small blackwater stream, c. 950 m., Ulu Sarawak, 15 Sept. 1932; coll. Oxford Exped. (1868).

The only allied species is the Ceylonese *D. fasciculatum*, which differs at once in the entire leaves. The dentation here is remarkable; the teeth are large, each formed of several cells similar to those of the lamina; the teeth of varied forms, obtuse, acute, recurved, larger or smaller, sometimes two close together and in slightly different planes so as to be almost bigeminate. The leaves are slightly contracted above the short wide base, then somewhat broadened above; the apex varies greatly in degree of its acuteness, the perichaetial leaves becoming upwards more and more acute, entire, and longly aristate.

### POLYTRICHACEAE.

*RHACELOPUS PILIFER* Bry. jav.

Stones in shade near waterfall, under 300 m., G. Dulit, Sarawak, 6 Aug. 1932; coll. Oxford Exped. (1143).

*PSEUDORHACELOPUS BORNEËNSIS* Dix., sp. n. (Pl. 4, fig. 51.)

A *P. philippinensi* Broth. differt caulibus *multo brevioribus*, minusquam 1 cm. altis; foliis e basi *dilatata, membranacea* in laminam *multo angustiore*, linguato-lanceolatam angustatis, acutioribus, saepius ob cellulam terminalem *spinosis, irregulariter grosse dentatis*, cellulis *multo laxioribus*, 20–22  $\mu$  latis, et setae papillis *angustioribus, altioribus, acutioribus*.

Fructus similis videtur.

*Hab.* Bettotan, near Sandakan, 21 Aug. 1927; coll. C. Boden Kloss (19171), type. Boulder in shade in stream-bed, under 300 m., G. Dulit, Sarawak, 15 Aug. 1932; coll. Oxford Exped. (1287).

Quite distinct from the *P. philippinensis* Broth. in the characters above given. *P. Peteloti* Thér. & Henr. differs from both in the quite entire leaves, *P. latifolius* Thér. & Henr., also from Tonkin, in the very broad, obtusely rounded leaves. The Bornean *R. acaulis* Mitt., which I have not seen, is described as with leaves 'integerrima', only the perichaetial leaves 'apice paucidentata'.

**POGONATUM JUNGHUHNIANUM** (Doz. & Molk.) Bry. jav.

Near Dallas, c. 900 m., Brit. N. Borneo, 5 Nov. 1931 ; coll. Holttum (25256). Kemoel, W. Koetai, Oct. 1925 ; coll. F. H. Endert (3924), Herb. Hort. Bot. Bog. (2587). A tall, very strict form with long straight setae.

New to Borneo. *Distr.* Wide.

**POGONATUM CIRCATUM** (Sw.) Brid.

In white sand forest, 800–900 m., Ulu Koyan, Sarawak, 16 Sept. 1932 ; coll. Oxford Exped. (1876). *Ibidem*, c. 1,200 m., Dulit Ridge (1878).

**POGONATUM MACROPHYILLOIDES** Broth.

Kemoel, W. Koetai, Oct. 1925 ; coll. F. H. Endert (3858), Herb. Hort. Bot. Bog. (2547).

**POGONATUM EURYPHYLLUM** Dix., sp. n. (Pl. 4, fig. 52.)

Robustum. Caulis elatus, ad 12 cm. altus, validus, aetate inferne nudus. Folia conferta, madida patentia, sicca *leniter flexuosa* ; *magna*, 10–14 mm. longa, superne usque ad 1.5 mm. lata ; a basi *brevissima dilatata late lingulata, vel leniter spatulata*, raptim *late acutata* ; margines e summa fere parte basilari infra spinulose, supra *grosse, aculeate*, spinoso-dentata. Costa inferne lata, male delimitata, superne *angusta*, dorso ad apicem parum dentata. Lamina superior bistratosa, ad marginem usque fere ad insertionem folii leniter *incrassata*. Lamellae parum conferta, *breves*, circa 2-seriatae, cellula superiore vix diversa rotundata vel subtruncata.

Fructus (unicus) setam 2.5 cm. altam, thecam majusculam, macrostomam deoperculatam exhibet.

*Hab.* Near Kamborangah, 2,200 m., Brit. N. Borneo, 13 Nov. 1931 ; coll. Holttum (25644), type. Tenompok, 1,300 m., 11 Nov. 1931 (25344).

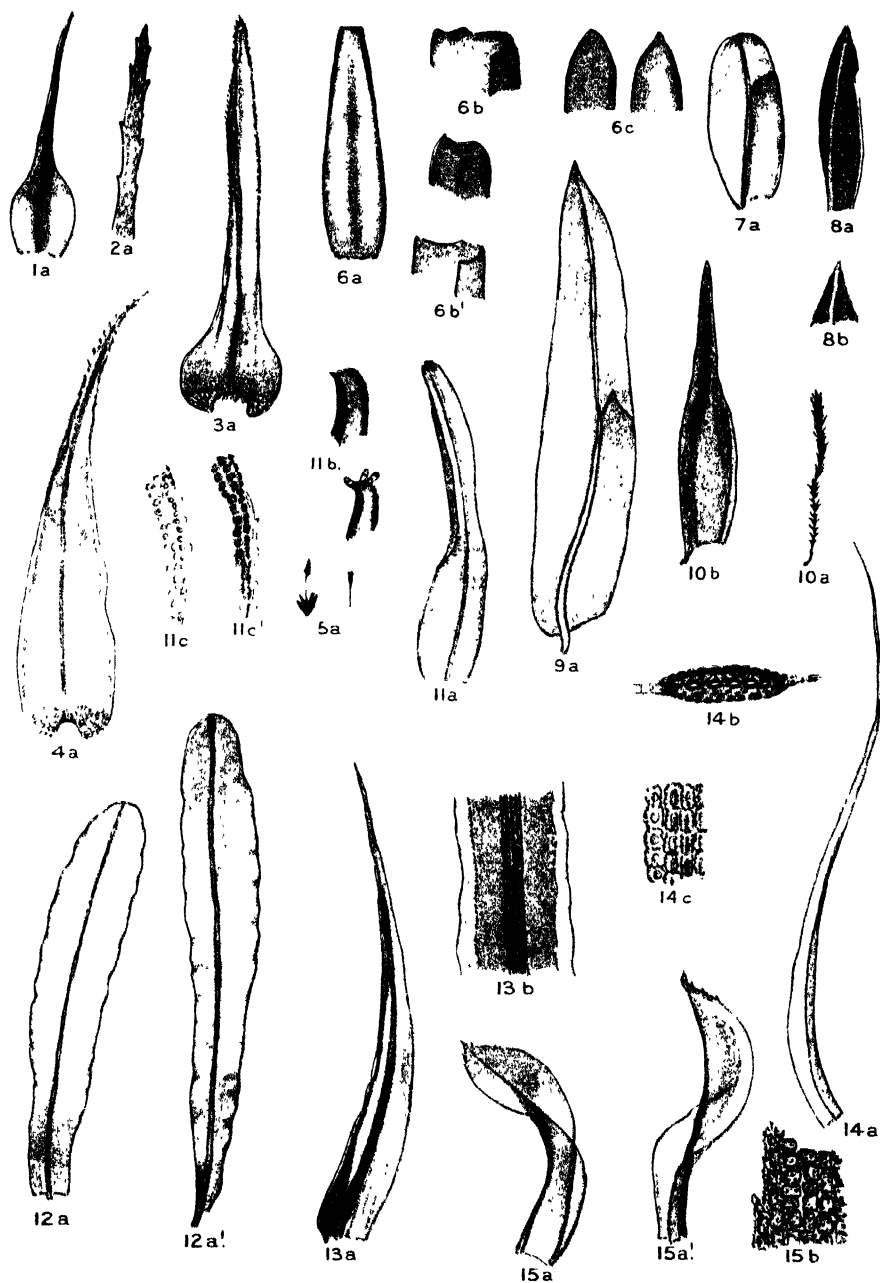
The very broad leaves in proportion to their length, not crisped when dry, give this a very distinct appearance. The coarse tooting and the thickening of the margin to a little above the insertion of the leaf are also marked characters. In the upper part of the leaf the marginal teeth, very broad at the base, are composed of many cells, similar to those of the lamina ; they are tipped by a single, much larger, acute, red cell.

**DAWSONIACEAE.****DAWSONIA ALTISSIMA** Geh.

Tenompok, c. 1,425 m., Brit. N. Borneo, 11 Nov. 1931 ; coll. Holttum (25343). *Ibidem*, between Lumu-Lumu and Kamborangah, 1,700 m., 13 Nov. 1931 (25642).

**DAWSONIA BREVIFOLIA** Gepp

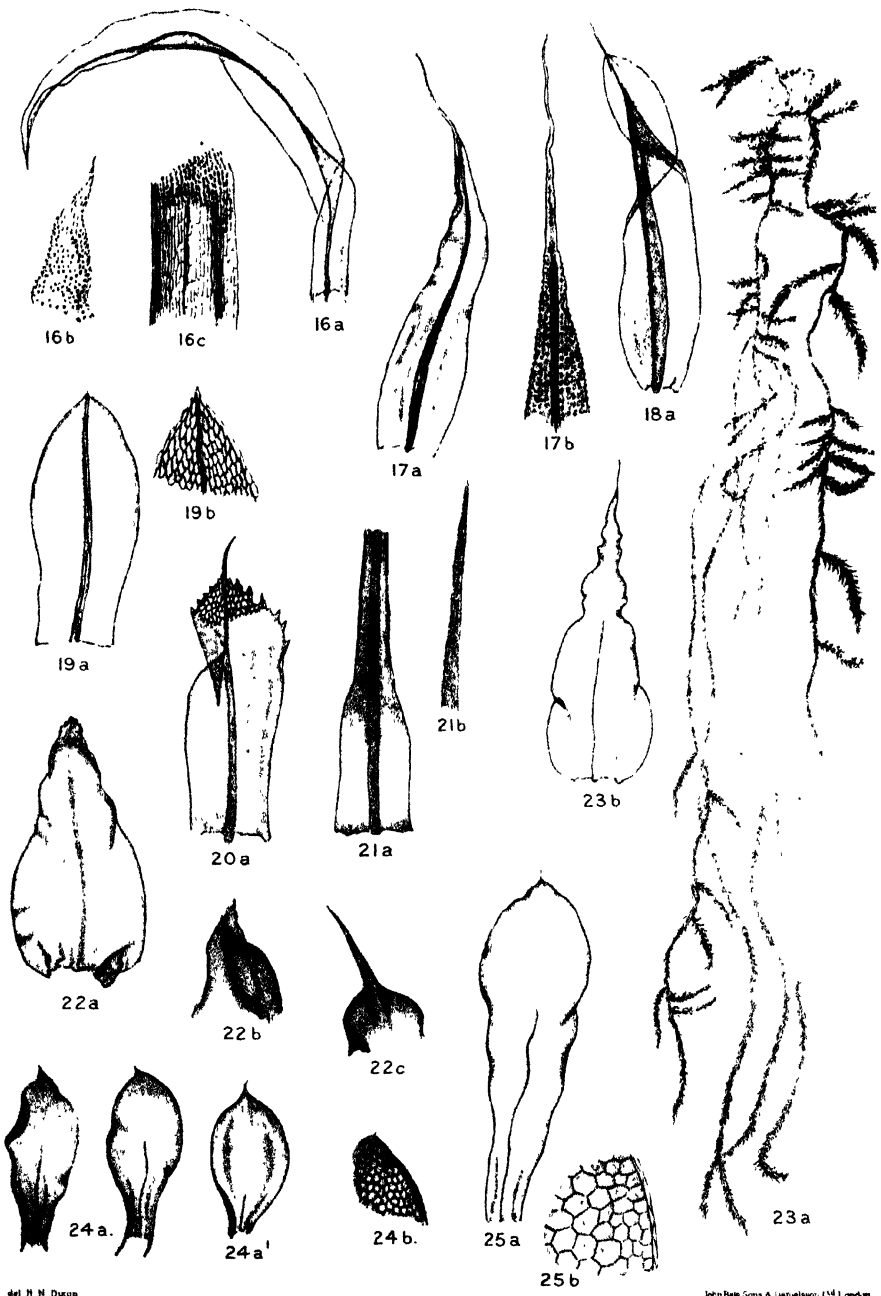
Tenompok, Brit. N. Borneo, 1,425 m., 11 Nov. 1931 ; coll. Holttum (25323), and Kinabalu, c. 2,750 m., 16 Nov. 1931 (A). Both of these the ♂ plant.



del H. N. Dixon

John Bale, Foss & [unclear] 1911 London

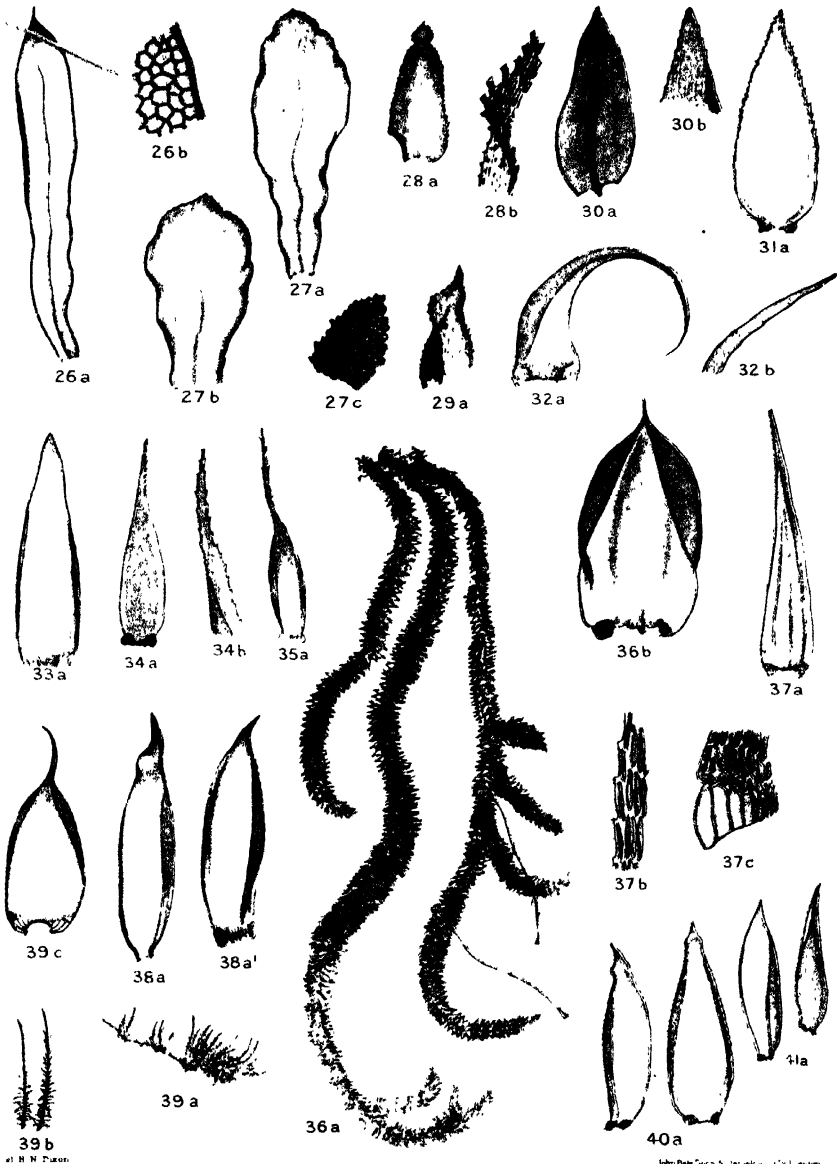




del. H. N. Dixon

John Ball, Gosport, Hampshire, L.M. London





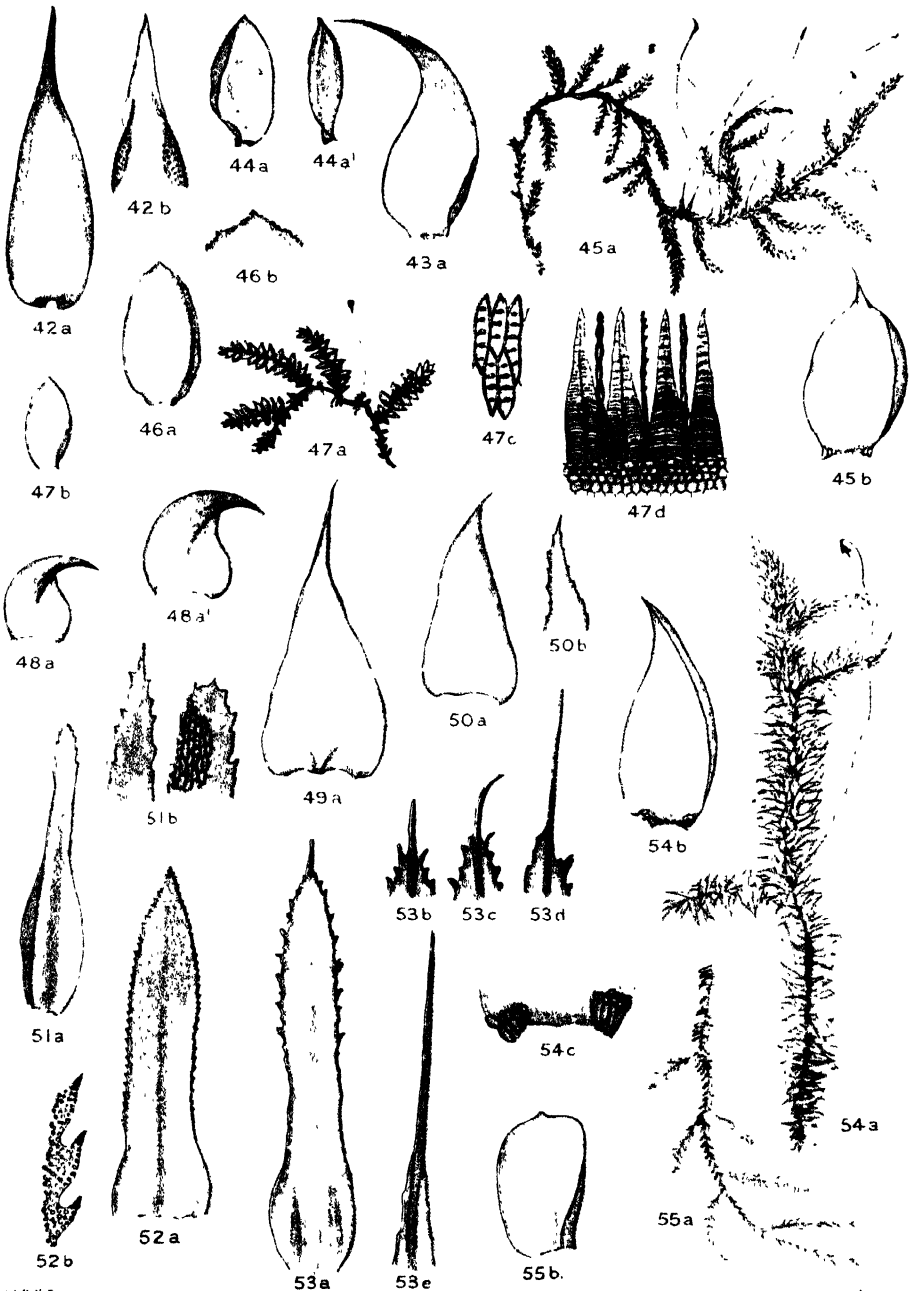
at H. N. Dixon.

John Bates Smith, N. H. Smith, and J. H. Smith.

BORNEO MOSSES







del R. H. Dixon

John Bannister A. C. (1913) London



Kinabalu, c. 2,450 m., 16 Nov. 1931 (25336). In fruit. The fruit has not been described. It does not appear to differ from that of *D. altissima* &c., but owing to the shortness of the leaves is much more conspicuous. Seta c. 2 cm. Theca, with operculum, rather over 1 cm.

## EXPLANATION OF THE PLATES.

## PLATE 1.

- Fig. 1. *Andreaea kinabaluensis*. *a*, leaf,  $\times 20$ .  
 Fig. 2. *Ditrichum spinulosum*. *a*, leaf-apex,  $\times 40$ .  
 Fig. 3. *Dicranoloma angustifrondeum*. *a*, leaf,  $\times 10$ .  
 Fig. 4. *Dicranoloma euryloma*. *a*, leaf,  $\times 10$ .  
 Fig. 5. *Cladopodanthus microcarpus*. *a*, fruit, young and mature,  $\times 2$ .  
 Fig. 6. *Cladopodanthus truncatus*. *a*, leaf,  $\times 10$ ; *b, b'*, leaf-apex,  $\times 40$ ; *c*, do. of apical leaves,  $\times 40$ .  
 Fig. 7. *Fissidens longevaginatus*. *a*, leaf,  $\times 20$ .  
 Fig. 8. *Fissidens albo-limbatus*. *a*, leaf,  $\times 20$ ; *b*, leaf-apex,  $\times 40$ .  
 Fig. 9. *Fissidens perpellucidus*. *a*, leaf,  $\times 20$ .  
 Fig. 10. *Fissidens pachyphyllus*. *a*, stem,  $\times 2$ ; *b*, leaf,  $\times 20$ .  
 Fig. 11. *Syrrhopodon Richardsii*. *a*, leaf,  $\times 20$ ; *b*, apices of leaves,  $\times 40$ ; *c, c*, border of leaf at shoulder,  $\times 100$ .  
 Fig. 12. *Calymperes sarawakense*. *a, a*, leaves,  $\times 20$ .  
 Fig. 13. *Chionoloma longifolium*. *a*, leaf,  $\times 10$ ; *b*, portion of mid-leaf,  $\times 40$ .  
 Fig. 14. *Stephanodictyon borneense*. *a*, leaf,  $\times 10$ ; *b*, nerve section,  $\times 150$ ; *c*, cells above base,  $\times 200$ .  
 Fig. 15. *Leptodontium kinabaluense*. *a, a'*, leaves,  $\times 20$ ; *b*, upper marginal cells,  $\times 200$ .

## PLATE 2.

- Fig. 16. *Leptodontopsis orientalis*. *a*, leaf,  $\times 20$ ; *b*, apex of leaf,  $\times 40$ ; *c*, right half of leaf-base,  $\times 40$ .  
 Fig. 17. *Macromitrium ochraceoides*. *a*, leaf,  $\times 20$ ; *b*, apex of leaf,  $\times 50$ .  
 Fig. 18. *Macromitrium perdensifolium*. *a*, leaf,  $\times 20$ .  
 Fig. 19. *Funaria borneensis*. *a*, leaf,  $\times 10$ ; *b*, apex of leaf,  $\times 20$ .  
 Fig. 20. *Tayloria borneensis*. *a*, leaf,  $\times 10$ .  
 Fig. 21. *Bartramia aurescens*. *a*, lower half of leaf,  $\times 20$ ; *b*, leaf-apex,  $\times 40$ .  
 Fig. 22. *Neolindbergia robusta*. *a*, leaf,  $\times 10$ ; *b*, leaf-apex, side view,  $\times 20$ ; *c*, apex of inner perichaetial leaf,  $\times 20$ .  
 Fig. 23. *Barbella decipiens*. *a*, part of plant, nat. size; *b*, leaf,  $\times 20$ .  
 Fig. 24. *Distichophyllum aciphyllum*. *a, a'*, leaves,  $\times 20$ ; *b*, upper cells,  $\times 80$ .  
 Fig. 25. *Distichophyllum angustifolium*. *a*, leaf,  $\times 20$ ; *b*, upper cells,  $\times 80$ .

## PLATE 3.

- Fig. 26. *Distichophyllum angustissimum*. *a*, leaf,  $\times 20$ ; *b*, upper cells,  $\times 80$ .  
 Fig. 27. *Distichophyllum denticulatum*. *a*, lateral, *b*, dorsal leaves,  $\times 20$ .  
 Fig. 28. *Chaetomitrium Everetti*. *a*, branch-leaf,  $\times 20$ ; *b*, upper margin,  $\times 100$ .  
 Fig. 29. *Chaetomitrium Beccarii*. *a*, leaf-apex,  $\times 50$ .  
 Fig. 30. *Rhynchostegiella opacifolia*. *a*, leaf,  $\times 20$ ; *b*, leaf-apex,  $\times 50$ .  
 Fig. 31. *Acanthocladium brevifolium*. *a*, stem-leaf,  $\times 20$ .  
 Fig. 32. *Mastopoma denticulatum*. *a*, leaf,  $\times 20$ ; *b*, leaf-apex,  $\times 80$ .  
 Fig. 33. *Warburgiella laticuspis*. *a*, leaf,  $\times 20$ .

- Fig. 34. *Clastobryella asperima*. *a*, leaf,  $\times 20$ ; *b*, leaf-apex,  $\times 40$ .  
 Fig. 35. *Clastobryella capillifolia*. *a*, leaf,  $\times 20$ .  
 Fig. 36. *Acroporium praelongum*. *a*, stem, nat. size; *b*, leaf,  $\times 10$ .  
 Fig. 37. *Pilecium acroporioides*. *a*, leaf,  $\times 20$ ; *b*, upper marginal cells,  $\times 200$ ; *c*, alar cells,  $\times 100$ .  
 Fig. 38. *Rhaphidostichum aquaticum*. *a*, *a'*, leaves,  $\times 20$ .  
 Fig. 39. *Acroporium ramuligerum*. *a*, stem, nat. size; *b*, branches,  $\times 2$ ; *c*, leaf,  $\times 20$ .  
 Fig. 40. *Trichosteleum Everetti*. *a*, leaves,  $\times 20$ .  
 Fig. 41. *Taxithelium convolutum*. *a*, leaves,  $\times 20$ .

## PLATE 4.

- Fig. 42. *Rhaphidostichum dubium*. *a*, stem-leaf,  $\times 20$ ; *b*, apex of branch-leaf,  $\times 30$ .  
 Fig. 43. *Trichosteleum flexuoso-hamatum*. *a*, stem-leaf,  $\times 20$ .  
 Fig. 44. *Trichosteleum inflexifolium*. *a*, *a'*, leaves,  $\times 20$ .  
 Fig. 45. *Trichosteleum procerum*. *a*, stem, nat. size; *b*, leaf,  $\times 20$ .  
 Fig. 46. *Taxithelium micro-similans*. *a*, leaf,  $\times 20$ ; *b*, apex of leaf,  $\times 40$ .  
 Fig. 47. *Taxitheliella Richardsii*. *a*, stem,  $\times 2$ ; *b*, leaf,  $\times 20$ ; *c*, cells,  $\times 200$ ; *d*, peristome,  $\times 120$ ; left dorsal, right ventral view.  
 Fig. 48. *Ectropothecium sublaticuspis*. *a*, *a'*, leaves,  $\times 20$ .  
 Fig. 49. *Ectropothecium turgidum*. *a*, leaf,  $\times 20$ .  
 Fig. 50. *Ectropothecium dentatum*. *a*, stem-leaf,  $\times 20$ ; *b*, apex of branch-leaf,  $\times 40$ .  
 Fig. 51. *Pseudorhacelopus borneënsis*. *a*, leaf,  $\times 10$ ; *b*, leaf-apices,  $\times 40$ .  
 Fig. 52. *Pogonatum euryphyllum*. *a*, leaf,  $\times 5$ ; *b*, upper margin,  $\times 40$ .  
 Fig. 53. *Diphyscium rhynchophorum*. *a*, leaf,  $\times 10$ ; *b*, *c*, leaf-apices,  $\times 20$ ; *d*, *e*, do: of floral leaves,  $\times 20$ .  
 Fig. 54. *Acroporium macro-turgidum*. *a*, stem, nat. size; *b*, leaf,  $\times 5$ ; *c*, alar cells,  $\times 15$ .  
 Fig. 55. *Neckeropsis plagiochiloides*. *a*, part of stem, nat. size; *b*, leaf,  $\times 10$ .

The inheritance of a substance in the roots of seedling hybrid derivatives of *Lolium perenne* L.  $\times$  *Lolium multiflorum* Lam. causing a fluorescence reaction visible in filter-paper by screened ultra-violet light. By A. H. WOODFORDE, F.L.S., Department of Agriculture, Tasmania.

[Read 10 January 1935]

### INTRODUCTION.

Recent investigation by Linehan and Mercer (1) and Foy (2) indicates that the degree of potential perenniality of certain seed-strains of perennial rye-grass (*Lolium perenne* L.) may readily be determined by laboratory test. The method involves the examination by screened ultra-violet light of wavelength 3,000–4,000 Angstrom units, of seedlings grown on white filter-paper. Lack of perenniality is held to be correlated with a certain proportion of seedlings, which, when so examined, cause the filter-paper to exhibit a characteristic fluorescence. The name false, or pseudo-perennial, has been applied to such strains, and they are considered to have been derived from natural intercrossing of *L. perenne* and *L. multiflorum*, which have, in many instances, been sown together in pastures used for seed-production.

Gentner (3) and others have shown that the roots of Italian rye-grass when grown in contact with white filter-paper produce a substance which exhibits fluorescence. Foy (2) supposes this substance to be the product of a reaction between an exudate of unknown composition from the roots and certain matter contained in the filter-paper.

*Note.*—In order to achieve simplicity of expression the terms 'fluorescent' or 'fluorescence' are here used to indicate the presence in seedling roots of the substance which causes fluorescence in filter-paper. Similarly, seedlings whose roots do not contain the causating substances are designated 'non-fluorescent'.

Gentner quotes no exceptions to the occurrence of 'fluorescence' in *Lolium multiflorum*, and Nilsson (4), though he has noted certain aberrants, concludes that the species is normally 'fluorescent'. Linehan and Mercer (1) examined 3,333 seedlings raised from awned seeds of *Lolium* spp. and found them all 'fluorescent'.

*Lolium perenne* has been found by the above authors to be normally 'non-fluorescent', though some exceptions have occurred. Linehan and Mercer found a number of aberrants among material which they examined, but state that many of them arose from seeds of *L. multiflorum* whose awns had been lost.

The investigation herein reported was initiated in the autumn of 1932. The objects of the work were (1) to determine whether the root-substance

to which fluorescence is due is inheritable, (2) to study the inheritance of the root-substance which causes fluorescence, and (3) to test the theory that individuals whose roots contain the substance which causes fluorescence arise in strains of perennial rye-grass by hybridization with annual species. A preliminary note on the work appeared in the 'Tasmanian Journal of Agriculture', vol. iv, no. 3, August 1933.

In the meantime, Corkhill (5) published a note on a selfing experiment with typical 'false' perennial rye-grass plants. He reported a segregation ratio closely approximating three 'fluorescent' to one 'non-fluorescent'. Some time later Linehan and Mercer (6) gave a summary of the results of a hybridization experiment along similar lines to that herein discussed, and stated that 'fluorescence' was inherited as a simple Mendelian dominant. They found no linkage between 'fluorescence' and annual or biennial habit, but consider the fluorescent content of a strain of *L. perenne* a useful measure of agronomic merit. Shortly after publication by these authors Trumble and Phipps (7) reported a similar investigation in which Wimmera rye-grass and *Lolium perenne* were employed as parents. It is shown that Wimmera rye-grass, to which the botanical name *Lolium subulatum* has been applied, is an unfixed hybrid segregating 'fluorescent' and 'non-fluorescent'. 'Fluorescence' is shown to be inherited from the Wimmera parent as a dominant character dependent on one, or possibly two, genetic factors. The theory is advanced that Wimmera rye-grass arose by natural hybridism between the 'non-fluorescent' annual *Lolium rigidum* and *L. multiflorum*, and it is argued that the ultra-violet light test for perenniality may be misleading when Wimmera rye-grass is grown with, or in proximity to, perennial rye-grass.

Though much of the matter dealt with in this paper has already been discussed by the above authors, few actual data have been presented. The evidence here discussed should in any event prove of value in that it affords confirmation of the results now on record, while certain aspects of the situation may be presented which have not elsewhere been exhaustively dealt with.

#### SCOPE OF THE INVESTIGATION.

Nineteen plants of *L. perenne* were emasculated and hand-crossed in a glass-house with an equal number of plants of *L. multiflorum*. First and second generation material was subjected to the standard ultra-violet light test, and a considerable number of F<sub>2</sub> seedlings were transplanted into soil in boxes, from which they will later be transferred to a field experimental area for observation of their behaviour as regards perenniality.

#### MATERIAL AND METHODS.

Plant material was selected to conform with established botanical characters and with the most desirable agronomic types in both species. The features sought in the selected plants were :—

## 1. TAXONOMIC.

*L. perenne*. Shoots conduplicate in the bud. Flowering glumes awnless.

*L. multiflorum*. Shoots convolute in the bud. Flowering glumes awned.

## 2. AGRONOMIC.

*L. perenne*. Growth-form semi-erect. Leafage dense, relatively fine. Leaf-texture firm, colour dark green, culms few.

*L. multiflorum*. Growth-form erect, vigorous. Leaves broad, relatively lax, colour yellowish green.

The parents employed were raised from seed previously subjected to the standard ultra-violet light test. New Zealand Government certified first-harvest seed was used as the basis of the perennial (female) parentage, while the Italian (male) parents were derived from a commercial seed sample, also of New Zealand origin. Particulars relating to the proportion of 'fluorescent' and 'non-fluorescent' seedlings in each of the samples are set out below, viz. :—

Species.	No. of seedlings examined.	No. of fluorescent seedlings.	No. of non-fluorescent seedlings.	Percentage fluorescent seedlings.
<i>L. multiflorum</i> ....	376	332	44	88.3
<i>L. perenne</i> .....	386	8	378	2.1

Seventy-five plants of each species were planted out in pots in May 1932. A preliminary selection was made in October, and twenty-five plants of *L. perenne* were chosen as exemplifying as nearly as possible the ideal agronomic type. Many plants in the *L. multiflorum* group showed departure from normal characters, both taxonomic and agronomic, and the frequent occurrence of plants showing *L. perenne* characters gave rise at this stage to speculation regarding the purity of the strain. This variation, coupled with the occurrence of 'non-fluorescent' seedlings among the bulk lot of plants from which the *L. multiflorum* parents were selected, made it apparent that there had been some admixture of the plant stock with *L. perenne*, a view that was later confirmed by the fact that some of the plants used for pollinating the female florets gave rise, on selfing, to 'fluorescent' and 'non-fluorescent' progeny. It was considered, however, that the use of a limited amount of parent material heterozygous for 'fluorescence' was not likely to prejudice the results. The number of plants selected for crossing had finally to be reduced to nineteen, owing to the failure of six *L. perenne* plants to produce an inflorescence.

The technique of emasculation and pollination was that adopted by Jenkin (8). Three heads each reduced to twenty florets constituted a female unit, the remaining heads being bagged up for selfing. All the inflorescences which



appeared on the male parent plants were enclosed, and pollen was extracted from the creases in the bags for fertilizing the emasculated female florets. Glascine bags 12 inches by 6 were used for covering, and these were made pollen-proof at the open end by winding cotton-wool round the stems of the inflorescences and tying the mouths of the bags securely over the wool with raffia. The two species were totally isolated from each other in different sections of the glass-house, of which all windows and roof-vents were closed for an hour before and during emasculation and pollination.

Seed-germination was induced by means of a Copenhagen tank operated at a temperature of 18°–25° Centigrade. The seeds were widely spaced on 3-inch circular disks of Whatman filter-paper, not more than ten to a disk. Examination for fluorescence was made at intervals up to the eighteenth day, employing a table-model Hanovia analytic quartz mercury-vapour lamp having a dark filter interposed between the burner and the inspection chamber.

*Ultra-violet light inspection of first generation material.*

614 seeds resulted from the nineteen crosses, representing an average of 32.3 per female unit, or an average 'take' of 53.8 per cent. 543 seeds produced seedlings, and 71 failed to germinate, the percentage of germination thus being 88.4. The results of examination of  $F_1$  and  $P_1$  progeny are summarized in Table I. The data have been arranged in two groups, one (group 1) comprising ten crosses giving a population of 267 seedlings, all 'fluorescent', and the other (group 2) nine crosses resulting in 155 'fluorescent' and 121 'non-fluorescent' seedlings. This grouping of the data suggests itself by reason of the fact that a considerable body of the material carrying the dominant factor proved to be heterozygous for 'fluorescence', and the placing together in group 2 of the results obtained from the use of these parents gives emphasis to their consistency with those of group 1, in which it will be shown that homozygous material was involved.

*Examination of seedlings resulting from self-fertilization of  
L. multiflorum parents.*

In group 1 six plants produced all 'fluorescent' progeny. Plants M 146 and M 135 are obviously homozygous. It is doubtful if significant numbers of seeds were secured from the other four plants which selfed, but comparison of the results obtained from the crosses in which these were concerned with those involving M 146 and M 135 and with those of group 2 shows that they and the four plants which failed to self were also homozygous.

In group 2 five plants produced 'fluorescent' and 'non-fluorescent' progeny when selfed. Three were self-sterile, and one gave all 'fluorescent' progeny. All the plants involved in this group were heterozygous with the exception of M 59.

TABLE I.—Showing number of fluorescent and non-fluorescent seedling progeny of all crosses and of parent material. First generation.

P <sub>1</sub> Perennial plant no.	Fluorescent.	Non-fluorescent.	Seeds, infertile.	Total.	P <sub>1</sub> Italian plant no.	Fluorescent.	Non-fluorescent.	Seeds, infertile.	Total.	F <sub>1</sub>	Fluorescent.	Non-fluorescent.	Seeds, infertile.	Total.
<b>GROUP 1.</b>														
P 14	..	..	..	..	M 146	57	..	7	64	P. M.	26	..	2	28
P 8	..	14	..	14	M 87	14	..	..	14	14 × 146	39	..	1	40
P 105	..	..	..	..	M 55	12	..	1	13	8 × 87	18	..	..	18
P 15	..	..	..	..	M 97	..	..	..	..	105 × 55	23	..	8	31
P 34	..	..	..	..	M 64	..	..	..	..	15 × 97	28	..	1	29
P 104	..	..	..	..	M 80	..	..	..	..	34 × 64	30	..	2	32
P 40	..	..	..	..	M 52	..	..	..	..	104 × 80	17	..	6	23
P 3	..	3	..	3	M 61	9	..	..	9	40 × 52	28	..	9	37
P 35	..	2	2	4	M 56	15	..	2	17	3 × 61	42	..	5	47
P 10	..	..	..	..	M 135	35	..	3	38	35 × 56	16	..	2	18
	..	19	2	21		142	..	13	155	10 × 135	267	..	36	303
<b>GROUP 2.</b>														
P 7	..	..	..	..	M 75	5	..	..	8	P. M.	39	10	2	51
P 111	..	11	..	11	M 59	16	3	..	16	7 × 75	19	12	12	43
P 5	..	5	..	5	M 74	5	..	..	8	111 × 59	17	20	3	40
P 19	..	6	3	9	M 70	4	1	..	5	5 × 74	10	15	1	26
P 23	..	2	..	2	M 127	1	5	..	6	19 × 70	17	7	4	28
P 12	..	..	..	..	M 66	2	3	..	5	23 × 127	11	21	4	36
P 18	..	..	..	..	M 63	..	..	..	..	12 × 66	14	17	..	31
P 103	..	..	..	..	M 81	..	..	..	..	18 × 63	18	7	1	26
P 50	..	8	..	8	M 63	..	..	..	..	103 × 81	10	12	8	30
	..	32	3	35		33	15	..	48	50 × 63	155	121	35	311

RATIO (fluorescent to non-fluorescent).

Group 1 (10 crosses). 267 : 0. Fluorescence completely dominant.

Group 2 ( 9 crosses). 155 : 121 = 1.3 : 1.

*Seedlings resulting from self-fertilization of L. perenne parents.*

Only three of the ten parents employed in group 1 and five in group 2 produced seed from selfing, and the highest number of seeds obtained from one plant was fourteen (plant no. P 8). Although these numbers are probably insignificant individually, in the aggregate they must be considered significant, since, of a total of 51 seedlings, none exhibited 'fluorescence'. Moreover, the low percentage of 'fluorescence' (2.1) resulting from the ultra-violet light test of the seed from which the plants were raised lends support to the assumption that all, or practically all, of the *L. perenne* parents were 'non-fluorescent'.

*Ultra-violet light examination of second generation material.*

Sixty 'fluorescent' and 'non-fluorescent' hybrid seedlings were transplanted from the filter-paper germinating pads in order to study plant characters and to secure plants for study of the second generation. The following particulars indicate the parentage of the material from which seed was obtained for the determination of  $F_2$  segregation ratios and for the confirmation of the classification of hybrid plants designated 'non-fluorescent', viz. :—

Hybrid plant no.	Character.	Parents.
C 5-2	F	P 8 × M 87
C 5-3		
C 5-4		
C 5-5		
C 5-7		
C 5-8		
C 5-9		
C 5-10		
C 1-1	F	P 7 × M 75
C 11-1	f	P 18 × M 63
C 11-4	f	do.

F denotes 'fluorescent'.      f denotes 'non-fluorescent'.

In addition to the above material, the three 'non-fluorescent' plants which resulted from selfing the Italian parent M 66 were grown on.

It was anticipated that difficulty would be experienced in obtaining sufficient seeds by selfing to give significant segregation ratios. For this reason it was decided, as well as selfing the selected 'fluorescent' material, to isolate in pairs two related and two unrelated 'fluorescent' hybrid plants for mutual pollination. For this purpose plants C 5-9 and C 5-8 were bagged in one series, and C 5-10 and C 1-1 in another. The majority of the hybrid plants failed entirely to self, and, as expected, those which were partially self-fertile gave, with one exception, a very light setting of seed.

In order to obtain confirmatory evidence one plant in each of the selected groups of material, with the exception of the cross P 7 × M 75, was back-crossed to *L. perenne*.

The results of examination of material obtained by selfing and mutual pollination are tabulated in Tables II and III, while the classification of 'fluorescent' and 'non-fluorescent' seedlings obtained by back-crossing are set out in Table IV.

TABLE II.—*Classification of fluorescent and 'non-fluorescent' seedlings obtained from 'fluorescent' hybrid plants (a) by self-fertilization and (b) by mutual pollination.*

Pedigree no.	Parents.	Number of seedlings.			Percentage germination.
		Fluorescent.	Non-fluorescent.	Total.	
SELF-FERTILIZATION.					
C 5-4 .....	P 8 × M 87	20	4	24	96
C 5-5 .....	do.	15	5	20	95
C 5-2 .....	do.	2	1	3	100
C 5-7 .....	do.	3	0	3	100
C 5-3 .....	do.	10	2	12	100
MUTUAL POLLINATION.					
C 5-9 .....	do.	177	56	233	98
C 5-8 .....	do.				
C 5-10 .....	do.	155	43	198	99
C 1-1 .....	P 7 × M 75				
Total observed .....		382	111	493	
Calculated 3 : 1 .....		369.75	123.25	493	

Ratio obtained ..... 3.4 : 1.

TABLE III.—*Result of examination by ultra-violet light of seedlings obtained from self-fertilized 'non-fluorescent' F<sub>1</sub> and P<sub>1</sub> plants.*

Pedigree no.	Parents.	Number of seedlings.			Percentage germination.
		Fluorescent.	Non-fluorescent.	Total.	
C 11-1 .....	P 18 × M 63	2	4	6	85.7
C 11-4 .....	do.	1	1	2	66.6
	M 66-1	..	39	39	100
		3 *	44	47	

\* The 'fluorescence' which was observed in these three seedlings is assumed to have resulted from contamination.

TABLE IV.—*Classification of 'fluorescent' and 'non-fluorescent' seedlings resulting from back-crosses of 'fluorescent' and 'non-fluorescent' hybrid and P<sub>1</sub> plants to Lolium perenne.*

Pedigree no.	Parents.	Character.	Crossed to.	Fluor. seedlings.	Non-fluor. seedlings.	Total.	Percentage germination.
C 5-5 . . . .	P 8 × M 87	F*	P 2 A	54	47	101	98
		Observed . . . . .		54	47	101	
		Calculated 1 : 1 . . . .		50.5	50.5	101	
C 11-1 . . .	P 18 × M 63	f†	P 3 A	..	45	45	95.7
	66-1	f†	P 6 A	..	56	56	100

\* Indicates 'fluorescent'.

† Indicates 'non-fluorescent'.

## DISCUSSION OF THE RESULTS.

From the foregoing data it is clear that 'fluorescence' is inherited as a dominant character dependent on a single factor. In F<sub>1</sub> 'fluorescence' was completely dominant in all but one cross employing homozygous parents; while the 1.3 : 1 ratio obtained in group 2 is consistent with theoretical expectation for simple dominance as the result of mating hybrid material to the recessive. In the single cross (P 111 × M 59) where inconsistent results were obtained the occurrence of apparently 'non-fluorescent' progeny is difficult to account for. It may, however, have been associated with low seedling vitality. The hybrid seed germinated poorly (72 per cent.), and seedling growth was extremely slow and lacking in vigour. Fluorescence did not develop until the twelfth day, and was so faint at all stages as to be almost imperceptible. It is possible that the twelve apparently negative seedlings were positively constituted individuals unable to produce a visible reaction owing to their low vitality. There is, however, no means of testing this suggestion, as, unfortunately, neither the seedlings nor their parents were preserved.

In F<sub>2</sub> an excellent fit to a 3 : 1 ratio was obtained from the material arising from self-fertilization of the 'fluorescent' hybrids and from the progeny of the two pairs of mutually pollinated plants, while on back-crossing the 'fluorescent' hybrid C 5-5 to *Lolium perenne* a good agreement to a 1 : 1 ratio was apparent. On back-crossing the 'non-fluorescent' hybrid C 11-1 and one of the 'non-fluorescent' plants (M 66-1) obtained by selfing the Italian parent M 66 to the recessive, a totally 'non-fluorescent' population was obtained, as also when M 66-1 was self-fertilized. Two 'non-fluorescent' hybrid plants (C 11-1 and C 11-4) when selfed produced 'fluorescent' and 'non-fluorescent' progeny, but it is almost certain that this was due once at least to contamination. In the other instance, only three seeds resulted from selfing, one of which failed to germinate.

## CONCLUSIONS.

The root-substance which causes fluorescence in filter-paper is transmissible and is inherited as a simple Mendelian dominant, dependent on a single factor. The theory of hybridization between short-lived and perennial rye-grass species on which the value of the ultra-violet light test depends is confirmed.

## ACCESSORY OBSERVATIONS.

A point of interest is the question of relationship between 'fluorescence' and the presence of awns on the flowering glumes. There is obviously no genetic linkage between these characters. A study of the hybrid material arising from the various crosses revealed the occurrence of 'fluorescent' and 'non-fluorescent' plants both with and without awns. Had the Italian parent material always been genetically pure it is likely that all the hybrids would have been awned. The contamination with *L. perenne* earlier referred to, however, was evidently responsible for the variation noted. Corkhill (5) draws attention to variation of awn characters in the material studied by him.

Though in general Italianate characters were dominant in the hybrid generation, there was a lack of evidence of complete dominance of the annual or biennial habit associated with *L. multiflorum*. All the hybrid plants made good recovery after seeding and cutting, and in the autumn following their planting were showing vigorous growth, though of typical 'pseudo'-perennial character, with a high ratio of stems to foliage. This lends support to the note by Linchan and Mercer that evidence of linkage between fluorescence and biennial habit is wanting. It is probable, however, that the method of culture in use has favoured a prolonged survival of the hybrid plants, and that they would have succumbed under the more rigorous conditions of pasture association and lack of moisture. Further study is required in this connexion.

## SUMMARY.

1. This paper reports the results of an investigation into the inheritance, in the roots of hybrid seedling derivatives of *Lolium perenne* L.  $\times$  *Lolium multiflorum* Lam., of a substance which causes a fluorescent reaction in white filter-paper in screened ultra-violet light.

2. Observations by other investigators suggest that ultra-violet light examination of filter-paper on which seedlings are growing provides a ready means of determination of the potential persistence of perennial rye-grass seed-strains. Lack of perenniality is considered to be associated with a certain proportion of seedlings whose roots cause the paper to exhibit fluorescence. The investigators consider that the short-lived strains so determined have been derived by natural intercrossing of *L. perenne* and *L. multiflorum*.

3. Hybridization experiments were carried out with selected plants of *L. perenne* and *L. multiflorum*. A variable hybrid generation was secured, and it is shown that this was due to heterozygosity of some of the parent material. A study of second generation material resulted in an observed segregation

ratio of 3.4 : 1 from 'fluorescent' hybrid material. Similar material when back-crossed to the recessive gave a ratio closely approximating 1 : 1. 'Non-fluorescent' hybrid and parent material, on crossing with recessive plants, gave a totally 'non-fluorescent' population.

4. 'Fluorescence' is a simple Mendelian dominant, inherited on a single factor basis.

5. The theory of hybridization, upon which depends the value of the ultra-violet light method of distinguishing between short-lived and persistent strains of perennial rye-grass seed, has been confirmed.

6. Italianate characters are dominant in the hybrid generation, but there is so far no evidence of complete dominance of the annual or biennial habit associated with *L. multiflorum*.

7. There is no genetic linkage between fluorescence and awned flowering glumes.

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## Alpine Desmids from British Columbia.

By NELLIE CARTER, D.Sc., F.L.S.\*.

(With 49 text-figures)

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THE material which forms the subject of this investigation was collected by Dr. W. R. Taylor and his colleagues at varying times during the years 1921-27. An account of the general algae, exclusive of diatoms and desmids, has already been published by Taylor (1928). The altitude from which the samples were taken was usually higher than the tree limit, about 7,000 ft. (referred to as alpine habitats), but a certain number were obtained from altitudes of 5,000 ft. or a little less (parkland). A full account of the type of country in which the collections were made will be found in Taylor (1928).

Considering the samples ecologically, a strict comparison between the yield of the parkland and alpine samples cannot be made, because the majority were taken from alpine situations, and these yielded a far greater number of species than the parkland samples; therefore the parkland flora is possibly not so well represented. The total number of samples collected was very great, and it was found necessary to mix some of the samples together. In doing this care was taken only to mix samples collected from similar habitats in the same locality. Four main localities were recognized, namely: Bald Mts., Eagle Pass, Glacier, and Quartz Creek (Purcell Range), cf. Taylor (1928). A few samples were also taken from other localities. The Bald Mts. region yielded far more species than the others, but this again may merely be due to the fact that more samples were taken there than from the others. In each region five different kinds of habitats were originally recognized: (1) lakes, (2) ditches and pools, (3) streams and rivulets, (4) wet rocks, (5) moss and *Vaucheria* beds. It was found later, however, that there was so much agreement in the desmid flora of pools, ditches, and moss or *Vaucheria* beds that it was advisable to consider all as one type of habitat. This habitat proved to be the most prolific one for desmids.

The following lists give a comparison of the Desmid flora of the same kind of habitat in alpine and in parkland situations, as indicated by Taylor's collections:—

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\* From the Botanical Dept., East London College.



## 1. LAKES.

## Parkland.

*Cosmarium depressum* var. *achondrum*, *C. minimum*, *C. Portianum*, *C. Quasillus* var. *americana*, *C. subcostatum*, *Staurastrum alternans*.

## Alpine.

*Gonatozygon monotaenium*, *Penium spirostriolatum*, *Olosterium abruptum* var. *brevius*, *C. Jenneri* var. *robustum*, *Euastrum pulchellum*, *E. verrucosum* and var. *planktonicum*, *Cosmarium Cucurbita*, *C. depressum* and var. *achondrum*, *C. granatum* formae, *C. Holmiense* var. *integrum*, *C. impressulum*, *C. minimum*, *C. sexnotatum*, *C. subcucumis*, *C. Turpinii* var. *eximium*, *Staurastrum Dickiei*, *S. natator* var. *rhomboideum*, *S. punctulatum* var. *Kjellmani*, *S. spongiosum*.

## 2. DITCHES, POOLS, AND MOSS OR VAUCHERIA BEDS.

*Spirotaenia obscura*, *Cylindrocystis Brebissonii* var. *minor*, *Euastrum bidentatum*, *Cosmarium asphaerosporum* var. *strigosum*, *C. conspersum* var. *latum*, *C. Cucurbita*, *C. cymatopleurum* var. *tyrolicum*, *C. galeritum*, *C. impressulum*, *C. laeve*, *C. nasutum*, *C. pokornyanum*, *C. pseudailanthoideum*, *C. subbaleum* f. *minor*, *C. Turpinii* var. *eximium*, *Staurastrum natator* var. *rhomboideum*.

*Cylindrocystis Brebissonii* var. *minor*, *Netrium Digitus*, *Olosterium abruptum* var. *brevius*, *Pleurotaenium coronatum*, *Tetmemorus laevis*, *Euastrum ampullaceum*, *E. ansatum*, *E. bidentatum*, *E. binale*, *E. denticulatum*, *E. Didelta*, *E. insulare*, *E. oblongum* var. *cephalophorum*, *E. verrucosum* and var. *planktonicum*, *Micrasterias papillifera* var. *glabra*, *M. truncata* forma, *Cosmarium amoenum*, *C. anceps*, *C. Askenasyi* var. *americana*, *C. caelatum* forma, *C. Cucurbita*, *C. cymatopleurum* var. *tyrolicum*, *C. depressum* var. *achondrum*, *C. difficile*, *C. elegantissimum* f. *minor*, *C. globosum*, *C. granatum* var. *elongatum*, *C. Hammeri* and var. *homologodermum*, *C. Holmiense* var. *integrum*, *C. impressulum*, *C. nasutum*, *C. Novae-Semliae* var. *sibericum*, *C. ochthodes* var. *amoebum*, *C. pokornyanum*, *C. rectangulare* var. *cambrense*, *C. sexnotatum* forma, *C. speciosum* and vars. *simplex*, *Rostafinskii*, and f. *trigona*, *C. subbaleum* f. *minor*, *C. subcucumis*, *C. subspeciosum*, *C. subtumidum*, *C. supraspeciosum*, *C. Taylori*, *C. Turpinii* var. *eximium*, *C. undulatum* var. *crenulatum*, *C. venustum*, *Arthrodesmus crassus*, *Staurastrum acarides*, *S. botrophilum*, *S. brachycerum*, *S. Brebissonii*, *S. Clepsydra*, *S. Dickiei*, *S. inflexum*, *S. insigne*, *S. margaritaceum* var. *alpinum*, *S. Meriani*, *S. muticum*, *S. natator* var. *rhomboideum*, *S. orbiculare* var. *extensum*,

## Parkland.

## Alpine.

*S. pachyrhynchum*, *S. polymorphum*, *S. punctulatum* var. *Kjellmani*, *S. scabrum*, *S. seacostatum*, *S. tetracerum*, *S. spongiosum*, *Euastridium verrucosum*.

The small yield of the Parkland samples may be due in part to the very small number of collections made.

## 3. STREAMS AND RIVULETS.

*Euastrum Didelta*, *Cosmarium Hammeri*, *C. Taylori*, *Staurastrum punctulatum* var. *Kjellmani*.

*Cylindrocystis Brebissonii* var. *minor*, *Netrium Digitus*, *Roya anglica* f. *major*, *Euastrum bidentatum*, *Cosmarium Askenasyi* var. *americana*, *C. binum*, *C. caelatum*, *C. formosulum*, *C. Hammeri*, *C. Holmiense* var. *integrum*, *C. impressulum*, *C. monochondrum*, *C. pericymatium*, *C. Portianum*, *C. scnotatum*, *C. speciosum* vars. *simplex* and *Rostafinskii*, *C. subcucumis*, *C. supraspeciosum*, *C. Turpinii* var. *eximium*, *Staurastrum acarides*, *S. Dickiei*, *S. dilatatum*, *S. Meriani*, *S. natator* var. *rhomboidum*, *S. punctulatum* var. *Kjellmani*.

## 4. WET ROCKS.

*Cylindrocystis crassa*, *Netrium Digitus*, *Closterium Venus*, *Cosmarium formosulum*, *C. impressulum*, *C. subcucumis*, *Staurastrum acarides*, *S. punctulatum* var. *Kjellmani*.

*Roya anglica* f. *major*, *Cosmarium Askenasyi* var. *americana*, *C. Cucurbita*, *C. formosulum*, *C. Holmiense* var. *integrum*, *C. pokornyianum*, *C. speciosum* and vars. *simplex* and *biforme*, *Staurastrum Meriani*.

The majority of the species found are such as have a cosmopolitan distribution, or else are already well known as alpine forms. Some of the desmids have already been recorded from British Columbia by Wailes (1925-33) and Wailes and Tiffany (1929). Geographically, the occurrence of two forms, *Cosmarium Askenasyi* var. *americana* and *C. supraspeciosum* is noteworthy. *C. Askenasyi* has long been known as a typical desmid of Australasia and the neighbouring regions; no form of it has hitherto been seen outside this part of the world. *Cosmarium supraspeciosum*, originally described by Wolle from the United States, has since been found in Sumatra (Schmidle, 1895 a), and Australia (Raciborski, 1892). It is interesting that these two desmids show the same kind of discontinuous distribution as certain angiosperms (cf. *Nicotiana*, Good, 1927). The discovery of *C. subbalteum* f. *minor* in Canada is also noteworthy; the type of this species was described from Africa, and as far as I know it has not been seen since. A peculiar new species of *Cosmarium*, resembling *Pleurotaenium* in its cell-form, but with totally different chloroplasts, is described and named after its collector, *C. Taylori*. Another form described for the first time is *Euastridium verrucosum*, this being the third species of the genus.

In the systematic list which follows the alpine and parkland localities for each species are given. Where it is apparent after consulting the papers of Wailes that the altitudinal distribution in British Columbia is wider than Taylor's samples indicate, the additional habitats of Wailes are added in order to make the records for each species more complete as far as altitude is concerned in this region. Species or varieties marked with an asterisk have not been observed by Wailes.

### Systematic.

#### SPIROTAENIA Bréb.

##### \*SPIROTAENIA OBSOURA Ralfs

Alpine moss beds, Bald Mts.

Previously known from U.S. and Canada. Norway at 2,400 ft. (Ström).

#### CYLINDROCYSTIS Menegh.

##### CYLINDROCYSTIS BREBISSEONII Menegh. var. MINOR West

Parkland or alpine pools or rivulets, Bald Mts., Glacier, Field, and Grizzly Creek ; often conjugating.

World-wide distribution. French Alps (Allorge, Deflandre).

##### CYLINDROCYSTIS CRASSA de Bary

Parkland pools, streams, rivulets, or wet rocks, Glacier, Grizzly Creek. Often with zygospores.

Known from U.S. and Norway up to 3,500 ft. (Ström).

#### NETRIUM Näg.

##### NETRIUM DIGITUS (Ehr.) I. & R.

Parkland or alpine pools or quiet ditches or rivulets, wet rocks, or moss or *Vaucheria* beds, Bald Mts., Glacier, and Eagle Pass.

Known from U.S. and Canada. Similar habitats in Norway up to about 4,000 ft. (Ström). French Alps (Allorge, Deflandre).

The specimens were small, about 60–120  $\mu$  long, 30–33  $\mu$  wide, but were otherwise typical.

#### ROYA W. & G. S. W.

##### \*ROYA ANGLICA West forma MAJOR. (Figs. 19, 20.)

Alpine rivulets or moss beds or wet rocks, Bald Mts.

The specimens were rather large (110–140  $\mu$  in length, about 11  $\mu$  wide), and the wall was slightly rugose ; otherwise there seemed to be no points of difference as compared with the English specimens. In some respects they resembled *R. obtusa* (Bréb.) West var. *montana* West, but differed in the more cylindrical form of the median part of the cells and in the more truncate apices. In the preserved material, end vacuoles could not be distinguished.

The distribution of *R. anglica* is not very well known. It was described from England, and has since been recorded in Germany. It is possible that it has been confused with *R. obtusa* var. *montana*. The latter species has been recorded from alpine situations in Norway (Ström) and also from the French Alps (Allorge). Neither species has hitherto been known from America.

GONATOZYGON De Bary

GONATOZYGON MONOTAENIUM de Bary

Alpine lakes, Bald Mts.

Known from U.S. and Norway, up to 3,500 ft. (Ström).

PENIUM Bréb.

PENIUM SPIROSTRIOLATUM Barker

Alpine lakes, Eagle Pass.

Known from Arctic Canada. Alpine situations in French Alps and Norway (Ström and Allorge).

CLOSTERIUM Nitzsch.

CLOSTERIUM ABRUPTUM West var. BREVIUS West

Alpine lakes and pools, Eagle Pass and Bald Mts.

Forms of this species are known from alpine situations in Norway and France (Ström and Allorge).

CLOSTERIUM JENNERI Ralfs var. ROBUSTUM West

Alpine lakes, Eagle Pass.

The typical form is known from Canada and U.S., and also from alpine situations in Norway and France (Ström and Allorge).

\*CLOSTERIUM LITORALE Gay

Golden and Stony Creek localities.

CLOSTERIUM VENUS Kütz.

Wet rocks, parkland, Eagle Pass. Alpine (Wailles 1930 a).

World-wide distribution; known from alpine Norway and the French Alps (Ström and Allorge).

PLEUROTAENIUM Näg.

PLEUROTAENIUM CORONATUM (Bréb.) Rab.

Alpine moss beds, Bald Mts. region. Parkland (Wailles & Tiffany 1929).

Known from U.S. and Canada; alpine situations in France and Norway (Deflandre and Ström).

## TETMEMORUS Ralfs

## TETMEMORUS LAEVIS (Kütz.) Ralfs

Alpine pools and ditches, Bald Mts. region. Parkland (Wailes 1930 a, 1932).

Known from U.S. and Canada. French Alps (Allorge, Deflandre).

## EUASTRUM Ehr.

## \*EUASTRUM AMPULLACEUM Ralfs

Alpine pools, Bald Mts.

Alpine Norway (Ström).

## EUASTRUM ANSATUM Ralfs

Alpine pools amongst Myxophyceae. Bald Mts. region. Parkland and lowland (Wailes 1930 a, 1932).

U.S. and Canada. Alpine Norway and France (Ström, Allorge, Deflandre).

## EUASTRUM BIDENTATUM Näg.

Alpine and parkland, lakes, pools, rivulets, or moss beds, Bald Mts., Canon Creek, Eagle Pass.

Arctic Canada (Lowe). Alpine Norway and France (Ström, Allorge).

## EUASTRUM BINALE (Turp.) Ehr.

Alpine moss and *Vaucheria* beds, Glacier. Parkland (Wailes & Tiffany 1929); lowland (Wailes 1930 a).

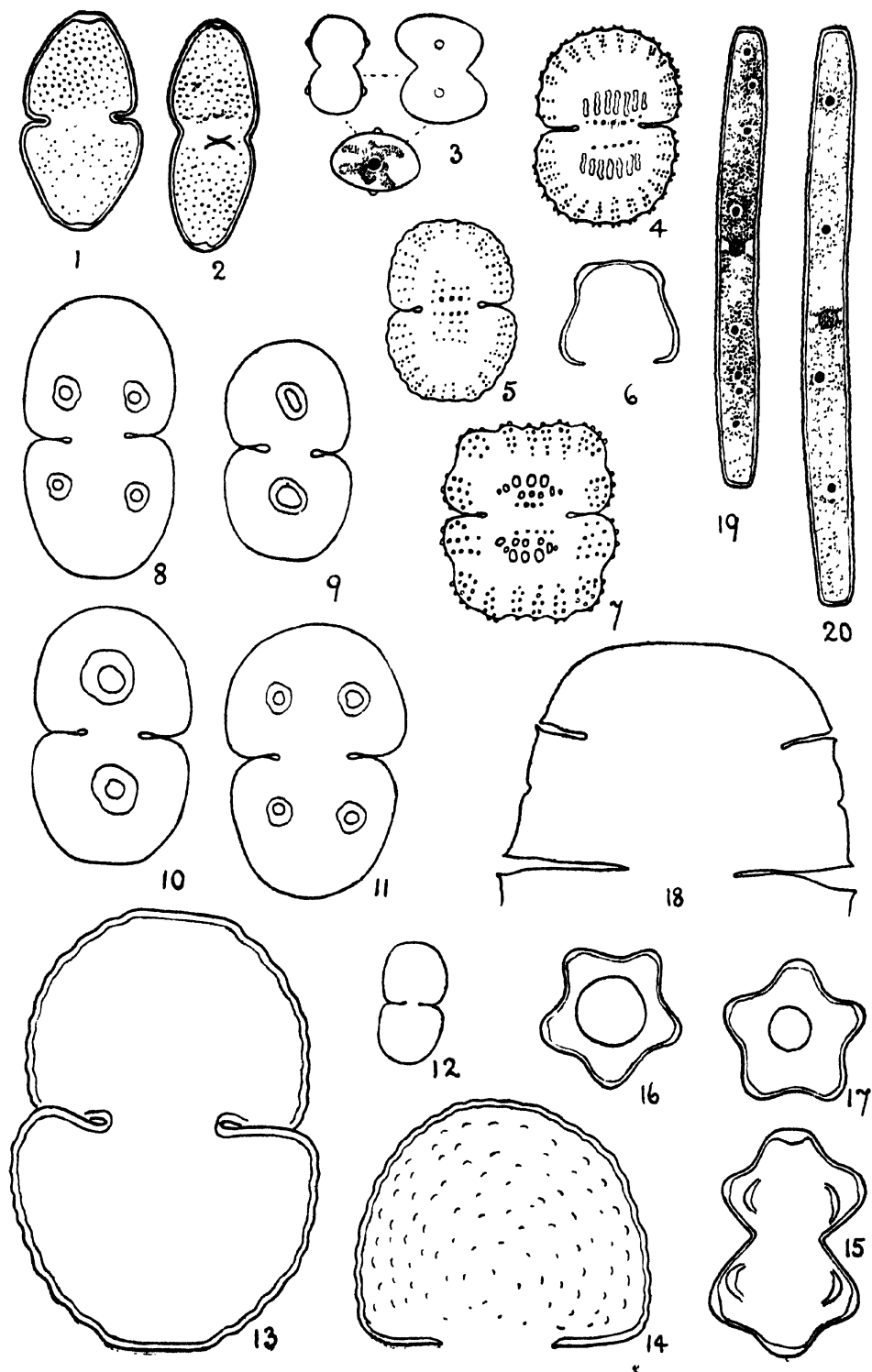
Alpine Norway and France (Ström, Allorge).

## EUASTRUM DENTICULATUM (Kirchn.) Gay

Alpine pools, Bald Mts. Parkland (Wailes & Tiffany 1929); lowland (Wailes 1930 a).

Alpine Norway and France (Ström, Allorge).

FIGS. 1-20.—1 & 2. *Cosmarium granatum* Bréb. var. *elongatum* Nordst., forma,  $\times 613$ . 3. *C. monochordrum* Nordst. forma West,  $\times 1,020$ . Showing front, side, and end views. 4. *C. binum* Nordst., forma,  $\times 613$ . 5. *C. formosulum* Hoff., forma,  $\times 613$ . 6. *C. Holmiense* Lund. var. *integrum* Lund.,  $\times 613$ . 7. *C. caelatum* Ralfs, forma,  $\times 613$ . 8-11. *C. subcucumis* Schmidle. Several individuals showing variation in the form of the cell and in the number and position of the pyrenoids, each of which is in the centre of a separate chloroplast,  $\times 613$ . 12. *C. rectangulare* Grun. var. *cambrense* West,  $\times 613$ . 13 & 14. *C. cymatopleurum* Nordst. var. *tyrolicum* Nordst., formae,  $\times 613$ . 15-17. *Stauroastrum insigne* Lund. 15, front view; 16, basal view of the semicell, showing the sinus; 17, vertical view showing the polar lobe;  $\times 1,070$ . 18. *Micrasterias crenata* Bréb., forma,  $\times 613$ . 19 & 20. *Roya anglica* West forma *major*,  $\times 613$ .



*EUASTRUM DIDELTA* (Turp.) Ralfs

In streams, parkland, Eagle Pass; alpine pools and moss beds, Bald Mts. and Quartz Creek. Lowland and alpine (Wailes 1930 *a* & *b*).

Alpine Norway and France (Ström, Allorge).

*EUASTRUM INSULARE* (Witttr.) Roy

Alpine pools, Bald Mts. Lowland (Wailes 1930 *a*).

French Alps (Allorge).

\**EUASTRUM OBLONGUM* (Grev.) Ralfs var. *CEPHALOPHORUM* West

Alpine pools, Bald Mts.

Alpine Norway (Ström).

*EUASTRUM PULCHELLUM* Bréb.

Alpine lakes, Bald Mts., and Eagle Pass.

French Alps (Allorge, Deflandre).

*EUASTRUM VERRUCOSUM* Ehr.

Alpine pools and quiet ditches, Bald Mts.

Alpine Norway (Ström); French Alps (Allorge).

\*Var. *PLANKTONICUM* West, forma.

Similar habitats to the typical form.

This is a very variable desmid. The variety was more frequent than the type. It differed from West's original alga in the greater development of the granules on the lobes of the semicell, which were produced to form short spines.

*MICRASTERIAS* Ag.*MICRASTERIAS PAPILLIFERA* Bréb. var. *GLABRA* Nordst.

Alpine pools, Bald Mts.

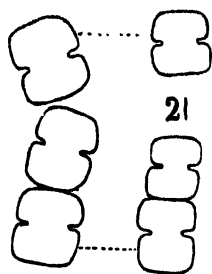
The type is known from alpine Norway and France (Ström, Allorge, and Deflandre); the variety was first described from Brazil and has since been recorded from the Sarek Mts. (Ström, 1923).

*MICRASTERIAS ORENATA* Bréb., forma. (Fig. 18.)

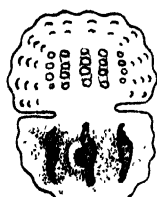
Alpine pools, quiet ditches, and moss beds, Bald Mts.

Alpine Norway and France (Ström, Allorge, and Deflandre).

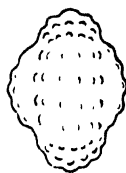
FIGS. 21-34.—21. *Cosmarium minimum* West, showing the tendency to form short filaments,  $\times 816$ . 22 & 23. *C. sexnotatum* Gutw., forma, front and end views,  $\times 850$ . 24-26. *C. pericymatium* Nordst. 24, front view, showing chloroplast; 25, vertical view; 26, side view:  $\times 850$ . 27 & 28. *C. Taylora*, sp. n. 28, shows the chloroplast,  $\times 490$ . 29 & 30. *Euastridium verrucosum*, sp. n. 29, vertical view; 30, front view:  $\times 850$ . 31 & 32. *Staurostrum natator* West var. *rhomboidum*, nov., biradial form. 31, front view; 32, end view:  $\times 850$ . 33 & 34. The same, tri-radial form. 33, front view; 34, vertical view:  $\times 850$ .



21



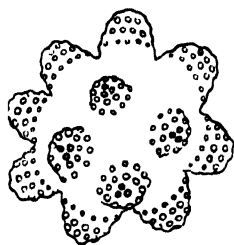
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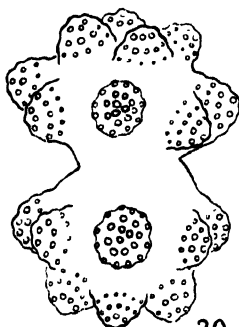
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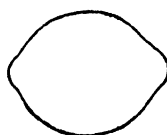
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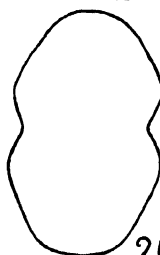
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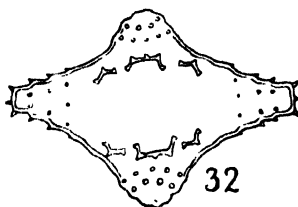
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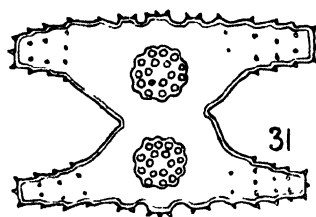
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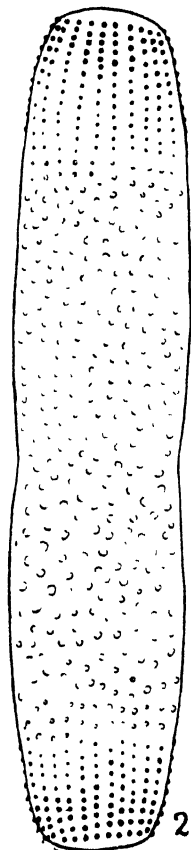
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32



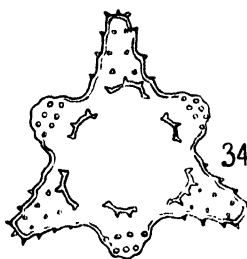
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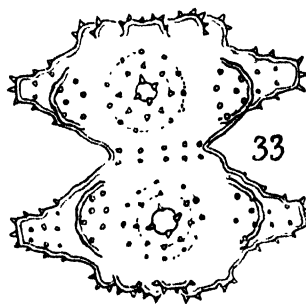
27



28



34



33



This is a very variable species and the alpine forms were not typical. The cells were relatively longer and the polar lobes larger, the upper incisions nearly horizontal, and the lateral lobes almost entire. In spite of these differences the desmid falls into this species rather than any other.

### COSMARIUM Corda

#### COSMARIUM AMOENUM Bréb.

Alpine pools with Myxophyceae or Chlorophyceae, or in alpine moss beds, Bald Mts. Parkland (Wailes and Tiffany 1929); lowland (Wailes 1930 a).

Alpine France and Norway (Allorge, Deflandre, and Ström).

#### COSMARIUM ANCEPS Lund.

Alpine pools, ditches, or moss beds, Bald Mts., Quartz Creek, and Canon Creek. Parkland (Wailes and Tiffany 1929).

Alpine France and Norway (Allorge, Deflandre, and Ström).

#### \*COSMARIUM ANNULATUM (Näg.) de Bary

Amongst *Nostoc*, cliffs below entrance of Canon Creek into Jordan Creek.

French Alps (Allorge).

#### \*COSMARIUM ASKENASYI Schmidle var. AMERICANA, nov. (Figs. 43-45.)

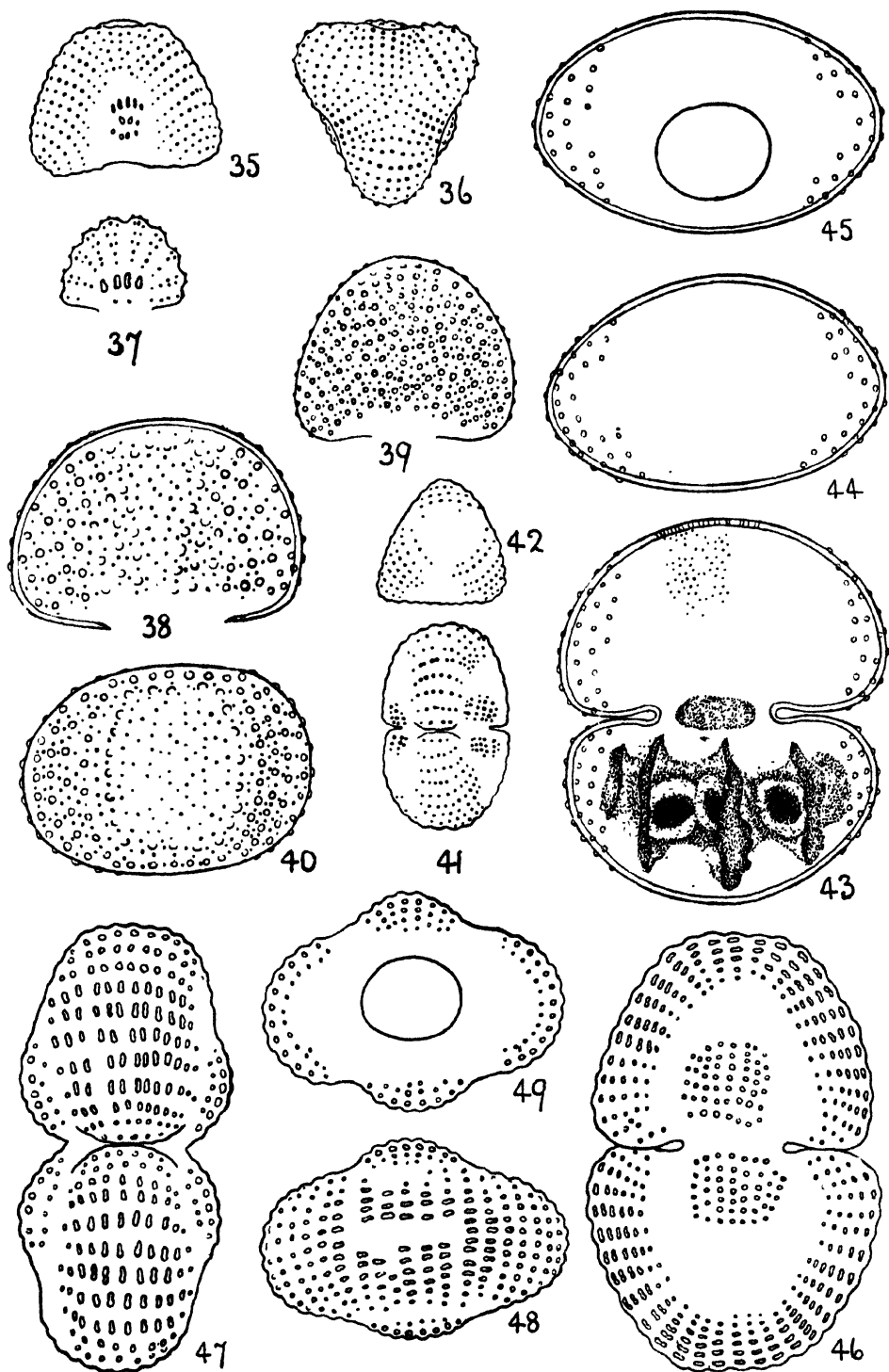
Var. minor, semicellulis reniformibus, granulis trans angulos basales multo delicatioribus quam in forma typica.

L. about 90  $\mu$ ; B. about 80  $\mu$ ; thickness about 50  $\mu$ ; isthmus about 30  $\mu$ .

Alpine or non-alpine situations; wet rocks, pools and ditches, rivulets, moss, and *Vaucheria* beds, Glacier and Bald Mts.

It was rather surprising to find this species, since the centre of its distribution seems to be Australasia and southern Asia. The points of difference between this alpine form and the type are so small, however, that there seems to be no justification for placing it in any other species. Its semicells are more depressed and consequently reniform, but this difference has been figured by Borge (1896) and others; the granulation is also more delicate, but this may possibly be related to its smaller size. So far as can be ascertained from

FIGS. 35-49.—35 & 36. *Cosmarium Quasillus* Lund. var. *americana* nov. forma *triquetra*. 35, front view of semicell; 36, end view:  $\times 613$ . 37. *C. nasutum* Nordst., forma. Front view of semicell,  $\times 613$ . 38-40. *C. subbalteum* Schmidle f. *minor*. 38 & 39, front view of semicell; 40, end view: 39,  $\times 613$ ; 38 & 40,  $\times 1,070$ . 41 & 42. *C. speciosum* Lund. forma *triquetra*. 41, front view; 42, vertical view:  $\times 613$ . 43-45. *C. Askenasyi* Schmidle var. *americana*, nov. 43, front view; 44, end view; 45, basal view of semicell, rather oblique, showing sinus:  $\times 613$ . 46-49. *C. supraspeciosum* Wille. 46, front view; 47, side view; 48, vertical view; 49, basal view, showing the sinus:  $\times 613$ .



existing figures, the chloroplasts in the American specimens are probably the same as in other forms of the species (cf. Schmidle, 1895 *a*, p. 304, f. 7 *a*, *b*; Gutwinski, 1902, t. 38, f. 45). Schmidle gives a description of the chloroplasts, but his figures are not good. He described two chloroplast plates, each with a pyrenoid, and sometimes each plate was split into two. Gutwinski's specimens agree rather better with my alga. The figure given by Bernard (1909, t. 3, f. 86) is rather misleading. In the American form there is a single axile chloroplast in each semicell, with two or more pyrenoids, and several plates radiating to the periphery. The type of chloroplast is the same as in *C. Ralfsii* (cf. Carter 1920). The cell-wall is punctate like the original form, but it seems to lack the central thickening of the face of the semicell figured by Schmidle and others. The discovery of this alga in America seems to show that *C. Askenasyi* has a peculiar type of discontinuous distribution, which is somewhat analogous to that shown by certain Phanerogams, e.g. *Nicotiana* (Good 1927).

*\*COSMARIUM ASPHAEROSPORUM* Nordst. var. *STRIGOSUM* Nordst.

Parkland and subalpine ditches and pools, Bald Mts.

*COSMARIUM BINUM* Nordst. (Fig. 4.)

Alpine rivulets amongst Myxophyceae, Bald Mts. Parkland (Wailes & Tiffany 1929).

This form was not exactly typical, being proportionately shorter and with only about 14 or 15 marginal crenations. A somewhat similar, but rather more depressed, form has been figured by Lowe (1923) from arctic Canada.

*COSMARIUM CAELATUM* Ralfs, formae. (Fig. 7.)

In ditches, pools, rivulets, wet moss, and *Vaucheria* beds, or on wet rocks, alpine, Bald Mts., Glacier, and Copperstain Lake D.

A widely distributed desmid, recorded from the mountains of France and Norway (Allorge, Deflandre, Ström). Ducellier (1916, p. 41) has pointed out how variable this species can be. Several variations of it were observed in the American material, one of which approximates to a form figured in Ducellier's fig. 2. Occurring in more than one sample, however, was a form which seems to differ from any other previously figured (see fig. 7). The granulation of the central tumour is very unusual, the upper lateral crenations are very large, and the two median apical crenations are smaller and with one granule only.

*\*COSMARIUM CONSPERSUM* Ralfs var. *LATUM* (Bréb.) West

Parkland pool, Canon Creek.

A widely distributed desmid, recorded from alpine France (Allorge, Deflandre).

*COSMARIUM CUCURBITA* Bréb.

Subalpine or alpine pools, ditches, or moss beds, or on irrorated rocks. Glacier and Bald Mts. Lowland (Wailes 1930 *a*).

Known from alpine situations in France and Norway (Ström, Deflandre).

*COSMARIUM CURTUM* (Bréb.) Ralfs

Field and Glacier.

Known from alpine France and Norway (Allorge, Deflandre, and Ström).

\**COSMARIUM CYMATOPLEURUM* Nordst. var. *TYROLICUM* Nordst., formae. (Figs. 13, 14.)

Parkland and alpine pools, Bald Mts., Quartz Creek, and Fish Lake regions.

Forms of this species commonly occur in alpine situations, but have not been recorded very frequently from America. Some specimens in the present collection were very similar to the figure given by West (1908, t. 65, f. 12), differing in the fact that the crenulations increase in size towards the apex of the semicell (see fig. 13); this form approximates to the var. *Archerii* (R. & B.) W. & G. S. W., except that the apex is not produced. A second form had more rounded semicells and more numerous crenulations of exceedingly delicate type and even arrangement (fig. 14). This shows some resemblance to Grönblad's form (1921, t. 6, f. 29). The extreme variability of this species has been noted by West (1908).

\**COSMARIUM DEPRESSUM* (Näg.) Lund. and var. *ACHONDRUM* (Boldt) West

Alpine and subalpine lakes and pools, Bald Mts.

Known from Canada and the United States (Lowe 1924), as well as from alpine France and Norway (Allorge, Ström).

\**COSMARIUM DIFFICILE* Lütke.

With other algae in alpine pools or moss beds, Bald Mts.

Already known from the United States and alpine France and Norway (Allorge, Ström).

\**COSMARIUM ELEGANTISSIMUM* Lund. f. *MINOR* West

Alpine pools and ditches, Bald Mts.

Both type and variety are already known from the United States, and the typical form is found in the French Alps (Allorge, Deflandre).

*COSMARIUM FORMOSULUM* Hoff., forma. (Fig. 5.)

With other algae in alpine or parkland rivulets or on wet or irrorated rocks. Recorded from high altitudes in France and Norway (Allorge, Ström).

This form differs from the typical alga (cf. West, iii, t. 88, f. 2) in its slightly longer cells and the much more delicate granulation of the central area.

*COSMARIUM GALERITUM* Nordst.

Parkland pool, Glacier, not common.

Known from alpine France and Norway (Deflandre, Ström).

**COSMARIUM GLOBOSUM** Bulnh.

Common in alpine pools and quiet ditches, Bald Mts. Parkland (Wailes & Tiffany 1929).

A desmid of world-wide distribution, recorded from arctic Canada (Lowe 1923) and from alpine France and Norway (Allorge, Ström).

**COSMARIUM GRANATUM** Bréb., formae.

Alpine lakes, Bald Mts.

An alga of world-wide distribution, recorded from alpine France and Norway (Allorge, Deflandre, Ström).

Var. **OCELLATUM** West (1895, p. 246, t. 15, f. 17).

Very rare in parkland and subalpine lakes, Bald Mts.

Var. **ELONGATUM** Nordst., forma. (Figs. 1, 2.)

Common in alpine moss beds, Bald Mts. and Glacier.

This form resembles Nordstedt's variety in its shallow isthmus, but is not so elongated. The slight apical thickening figured by West (ii, t. 63, f. 10) is also present.

**COSMARIUM HAMMERI** Reinsch

Alpine and subalpine pools and rivulets, Golden, Bald Mts., Quartz Creek, and Eagle Pass.

**\*Var. HOMALODERMUM** (Nordst.) West

In alpine pools, amongst *Vaucheria* or in moss beds, Bald Mts., Glacier, and Quartz Creek.

Both the type and the variety are known to favour high altitudes. The rather larger size and thick punctate walls of some individuals seem to justify their being placed under the var. *homalodermum*.

**\*COSMARIUM HOLMIENSE** Lund. var. **INTEGRUM** Lund. (Fig. 6.)

Alpine lakes and pools or rivulets, in moss or *Vaucheria* beds, or on irrorated rocks. Bald Mts., Glacier, and Field.

This alga, which was present in many samples, is known to occur in mountainous situations. Some specimens had a rather flat apex, and the four polar angles (two visible in the front view) were prominently thickened. Lowe (1923) has recorded it from arctic Canada.

**COSMARIUM IMPRESSULUM** Elfv.

Lakes, rivulets, wet rocks, or amongst mosses, Bald Mts., Quartz Creek, Canon Creek, Fish Lake, and Field. Alpine or parkland.

Recorded from alpine France and Norway (Allorge, Deflandre, Ström) and from arctic Canada (Lowe 1923).

**COSMARIUM LAEVE** Rabenh.

Amongst moss in pool, parkland, near Canon Creek. Alpine (Wailes 1920 b). Of world-wide distribution, recorded from alpine France (Allorge).

*\*COSMARIUM MINIMUM* West (Fig. 21.)

Alpine or parkland lakes or streams, Bald Mts.

This small alga occurred only in two samples, in one of which it was fairly abundant. The cells showed a slight tendency to adhere, forming very short filaments. It has some resemblance to *Spondylosium compactum* West (1902, t. 22, ff. 29, 30), but seems to lack the capacity to form definite filaments, the cells adhering together only temporarily.

*\*COSMARIUM MONOCHONDRUM* Nordst. forma West (1908, p. 104, t. 73, f. 26). (Fig. 3.)

Alpine rivulets, with other algae, Glacier.

The alga agreed with West's form in size and in general proportions, as well as in the breadth of the isthmus. The cells had the same general form, i.e. obversely semicircular, but differ in the more obtuse lateral margins which are not produced. This feature also affects the end view. *C. monochondrum* is not a common desmid (? only known from Scotland and Norway). Ström records it from alpine Norway.

*COSMARIUM NASUTUM* Nordst., forma. (Fig. 37.)

In pools or amongst mosses, alpine or subalpine, Bald Mts. and Canon Creek.

*C. nasutum* is known to be a rare desmid, characteristic of alpine situations. The American form differs from Nordstedt's original figure in the subdivision of the basal crenations and the granulation of the central tumour, which is ornamented by several elongated verrucae. Some of the individuals were almost identical with the figure given by Gutwinski (1909) of specimens from the Carpathians. Recorded from alpine France and Norway (Allorge, Deflandre, Ström).

*\*COSMARIUM NOVAE-SEMLIAE* Wille var. *SIBIRICUM* Boldt.

Alpine pools and ditches, Bald Mts.

Alpine France and Norway (Allorge, Ström).

*COSMARIUM OCHTHODES* Nordst. var. *AMOEBUM* West

Alpine pools or moss beds, Bald Mts.

*\*COSMARIUM PERICYMATIUM* Nordst. (Figs. 24-26.)

Alpine rivulets, Bald Mts.

The side-view of this species was rather more deeply constricted at the isthmus than figured by Nordstedt. It seems to be a typical upland form.

*\*COSMARIUM POKORNYANUM* (Grun.) West

Parkland or alpine, amongst mosses or on wet rocks, Canon Creek, Glacier, and Quartz Creek.

This has previously been known as a subalpine desmid. Lowe (1923) has recorded it from arctic Canada.

*\*COSMARIUM PSEUDATLANTHOIDEUM* West

Parkland, amongst mosses in pool, Golden.

Previously recorded from Colorado.

*COSMARIUM PORTIANUM* Arch.

Subalpine lakes, in rivulets or on wet rocks, Bald Mts. and Glacier.

A desmid of nearly world-wide distribution, known to be widely distributed in the United States. Recorded from alpine France and Norway (Allorge, Deflandre, Ström).

*\*COSMARIUM QUASILLUS* Lund. var. *AMERICANA* nov. forma *TRIQUETRA*. (Figs. 35, 36.)

Rare in subalpine lakes, Bald Mts.

Var. *apicibus haud elevatis at vix retusis*; *semicellulis pyramidatis truncatis, membrana granulata, granulis circiter 11 ad marginem lateralem unumquemque perspiciendis, ad apices vix conspicuis, granulis trans angulos basales oblique seriato-digestis sed ad apices verticaliter*; *tumere centrali granulis quam in forma typica paucioribus, superioribus subelongatis, praedito*. L.  $66\mu$ ; B.  $48\mu$ .

This alga, which, unfortunately, occurred only in one sample, differs from typical *C. Quasillus* in a number of features:—(1) in the apex not being produced, (2) in the even granulation of the lateral margins, (3) the more numerous peripheral granules, (4) the smaller number of granules in the central area. It bears a slight resemblance to var. *alpinum* Schmidle (1895*b*, p. 459), but differs (1) in the more angular pyramidal shape of the semicell, (2) in the greater number of granules round the margin, (3) in the elongation of the upper granules of the central area, (4) in the relatively narrower cells. Only the triquetral form was noticed and this was very rare.

*\*COSMARIUM RECTANGULARE* Grun. var. *CAMBRENSE* West (Fig. 12.)

Alpine pools with other algae, Bald Mts.

The typical form is known to be alpine.

*\*COSMARIUM SEXNOTATUM* Gutw., forma. (Figs. 22, 23.)

Lakes, pools, rivulets, or in moss beds, alpine. Bald Mts., Glacier, Eagle Pass, Field, and L. Louise.

The specimens differed from the type in the larger size of the central tumour, which showed at least five longitudinal series of granules. It was a very common desmid in the alpine samples, where it occurred in some abundance. Ström (1923) has recorded another form from Scandinavia (var. *tristriatum* (Lütke.) Schmidle).

*COSMARIUM SPECIOSUM* Lund.

Alpine pools, amongst *Vaucheria* or wet mosses, or on damp rocks, Bald Mts., Glacier, Canon Creek, and L. Louise. Parkland (Wailes & Tiffany 1929).

Recorded from similar alpine situations in the French Alps and in the mountains of Norway (Allorge, Deflandre, and Ström).

\***Forma TRIQUETRA.** (Figs. 41, 42.)

With the typical form, rare, amongst *Vaucheria* and mosses, at Glacier.

Var. **SIMPLEX** Nordst.

In rivulets and in similar situations to the above.

Var. **BIFORME** Nordst.

Alpine cliffs with *Nostoc*, Glacier. Parkland (Wailles & Tiffany 1929).

Var. **ROSTAFINSKII** (Gütw.) W. & G. S. W.

In rivulets and in similar situations to the preceding, and also at Quartz Creek.

This species, which is very variable, was very frequent, as might be expected in alpine situations.

\***COSMARIUM SUBBALTEUM** Schmidle (1898) forma **MINOR.** (Figs. 38–40.)

Alpine pools and moss beds, Bald Mts. and Quartz Creek; parkland, near Canon Creek.

This desmid, which was quite frequent in the Quartz Creek sample, bears some resemblance to *C. controversum* West in the form and granulation of its semicells. It differs, however, in the absence of a central tumour, the centre of the semicell being sometimes destitute of granules, as is also the apex and the region around the sinus. The cells are very variable in form, being sometimes pyramidal, sometimes nearly hemispherical. The vertical view differs greatly from *C. controversum*, since it is much more rectangular. The granules are interspersed with pores, which are usually distinctly visible, about five or six surrounding each granule, but with no very constant arrangement. The granules can be resolved as oblique rows across the basal angles of the semicell, but elsewhere a definite arrangement is difficult to distinguish. The position of the granules can be seen between the pores on the face of the semicells even when they themselves are not developed strongly. The desmid seems to show sufficiently the characters of *C. subbalteum* described by Schmidle from East Africa. The chief differences are (1) the smaller size, L. 50–88  $\mu$ ; B. 42–56  $\mu$ ; thickness, 28–40  $\mu$ ; isthmus, about 15  $\mu$  (Schmidle gives L. 108–120  $\mu$ ; B. 85–100  $\mu$ ); (2) the rather smaller number of granules round the margins; (3) the slightly deeper sinus. (1) and (2) can probably be correlated. So far as I know, *C. subbalteum* has not again been seen since Schmidle described it.

**COSMARIUM SUBCOSTATUM** Nordst.

Parkland lakes, Bald Mts. and amongst mosses near Canon Creek. Alpine (Wailles 1931 b).

Alpine Norway (Ström).



*COSMARIUM SUBOUCUMIS* Schmidle (Figs. 8-11.)

Parkland and more especially alpine lakes, rivulets, in moss beds, or on wet rocks, Bald Mts., Glacier, and near Canon Creek.

Known from alpine France and Norway (Allorge and Ström), and from arctic Canada (Lowe 1923).

This desmid, which occurred in several samples, showed slight variation in the form of its semicells, which are sometimes relatively longer and with parallel sides, at other times more gradually rounded. There was also variation in the cytoplasmic structure, some forms having a single chloroplast in each semicell with one pyrenoid in a central position, whilst other forms had two chloroplasts per semicell, each with a pyrenoid. Possibly these represent two distinct races, as they did not occur intermingled. The form with two chloroplasts and two pyrenoids in each semicell is, of course, the typical one.

*COSMARIUM SUBSPECIOSUM* Nordst.

Alpine moss beds, Bald Mts.

A typical habitat of this species.

*COSMARIUM SUBTUMIDUM* Nordst.

Alpine pools, Bald Mts., and Field. Parkland (Wailes 1932).

A desmid of nearly world-wide distribution.

\**COSMARIUM SUPRASPECIOSUM* Wolle (1884, t. 4, ff. 5, 6). (Figs. 46-49.)

Alpine pools, ditches, rivulets, or moss beds, Bald Mts., Glacier, and Quartz Creek.

This desmid was a frequent constituent of alpine samples in all localities. It is a beautiful species, with pyramidal truncate semicells and a broad inflation just above the sinus. The margin of the semicell shows about 24-28 undulations, the lower ones surmounted by a single granule, the upper lateral ones emarginate; the apical undulations are flattened and not so prominent. The front of the semicell is ornamented with series of granules radiating from the margin, but ending so as to leave a clear space around the central protuberance; the peripheral granules are emarginate. The basal protuberance has usually about eight (but up to twelve) vertical rows of granules, of which the lowest tend to be larger and more distant. The vertical view shows transverse series of granules at the ends, tending to disappear towards the centre. In the lateral view it is seen that the central tumour is very close to the sinus. It resembles *C. balteum* West (1896), but differs in the median inflation in the vertical view. L. about  $104\mu$ ; B. about  $70\mu$ ; thickness about  $50\mu$  (including tumour); isthmus about  $25\mu$ .

This desmid has been recorded, since Wolle first described it, by Raciborski (1892) and by Schmidle (1895 a) from Sumatra. Its discontinuous geographical distribution therefore shows some resemblance to that of *C. Askenasyi*.

**\*COSMARIUM TAYLORI, sp. n. (Figs. 27, 28.)**

Pools or rivulets, alpine or parkland, Bald Mts., and Glacier.

*Cosm. longum* cylindricum, cellulis 3-5-plo diametro longioribus, ad sinum vix constrictum, apicibus truncatum; granulis in seriebus verticalibus circiter 24 (12 a fronte visis) ad marginem superiorem semicellulae uniuscujusque digestis, in serie unaquaque granulis circiter 8 plane conspiciendis, ab sinum versus granula ita se minuunt ut membrana denique quasi scrobiculata fiat; chromatophoris axillaribus pyrenoidibus centralibus pluribus instructis.

L. 160-230  $\mu$ ; B. about 45-50  $\mu$ ; B. of apex about 35  $\mu$ ; B. of isthmus about 45  $\mu$ .

The specimens were in a very healthy condition and had abundant protoplasmic contents, which rendered an investigation of the cell-contents somewhat difficult. Staining showed, however, that the chloroplast is axile, with elaborate irregular radiating portions passing towards the cell-wall (cf. *C. pyramidatum* Carter 1920, t. 10, ff. 24, 25). The axile part of the chloroplast contains several pyrenoids.

This alga seems to be different from any desmid previously described. Its elaborate chloroplast precludes any relationship with *Penium* or *Pleurotaenium*. It differs from other elongated *Cosmarium* species previously described, such as *C. elongatum* Racib. and *C. pseudotinecense* Grönblad (1921), in its general cell-form, the granulation at the top of the semicell, and in its elaborate chloroplast.

**\*COSMARIUM TURPINII Bréb. var. EXIMIUM West**

In lakes, pools, or rivulets with other algae, or encrusting rocks, or amongst damp mosses; alpine or parkland, Bald Mts., Eagle Pass, and Canon Creek.

**\*COSMARIUM UNDULATUM Corda var. GRENULATUM (Näg.) Witttr.**

Alpine pools and moss beds, Bald Mts.

**COSMARIUM VENUSTUM (Bréb.) Arch.**

Alpine pools and moss beds, Bald Mts. and Glacier.

Alpine France and Norway (Allorge, Deflandre, Ström).

The alga was rather variable in the form of its cells, some possessing the pyramidalate semicells of the typical form, whilst others agreed more with var. *majus* of Wittrock in their more rectangular lateral lobes, although not being any larger than the type.

**ARTHRODESMUS Ehr.****\*ARTHRODESMUS CRASSUS West**

Alpine pools and quiet ditches, Bald Mts. and Quartz Creek.

**STAURASTRUM Meyen****STAURASTRUM ACARIDES Nordst.**

Alpine and parkland, pools, and rivulets, amongst algae or wet mosses, or

on damp rocks, Bald Mts. and Glacier. This is known to be an arctic alpine desmid, and has been recorded from high altitudes in France and Norway (Allorge, Ström).

*STAURASTRUM ALTERNANS* Bréb.

Parkland lakes, rare.

*STAURASTRUM BOTROPHILUM* Wolle

Alpine pools and moss beds, Bald Mts.

Recorded by Prescott (1931).

\**STAURASTRUM BRACHYCERUM* Bréb.

Common in alpine pools with other algae, Bald Mts.

*STAURASTRUM BREBISSEONII* Arch.

Alpine pools and moss beds, Bald Mts.

\**STAURASTRUM CLEPSYDRA* Nordst., forma.

Alpine pools and moss beds, Bald Mts.

This differed from the type in its slightly larger size (L.  $36\ \mu$ ) and in the rather more rounded angles, especially in the vertical view.

*STAURASTRUM DICKIEI* Ralfs

Alpine lakes, pools, rivulets, or moss beds, Bald Mts. Lowland (Wailes 1930a). Alpine France and Norway (Allorge, Deflandre, Ström).

*STAURASTRUM DILATATUM* Ehr.

Alpine rivulets, Glacier. Parkland (Wailes & Tiffany 1929).

\**STAURASTRUM INFLEXUM* Bréb.

Alpine moss beds, Bald Mts.

\**STAURASTRUM INSIGNE* Lund. (Figs. 15-17.)

Alpine pools and quiet ditches, Bald Mts.

This seems to be a characteristic alpine and arctic desmid, as the previous records of it would indicate. Except for Greenland, it has not been previously found outside Europe.

\**STAURASTRUM MARGARITACEUM* (Ehr.) Menegh. var. *ALPINUM* Schmidle

Alpine pools and wet rocks, Bald Mts.

*STAURASTRUM MERIANI* Reinsch

Alpine pools and rivulets, or amongst damp mosses or wet rocks, Bald Mts., Glacier, Quartz Creek, Fish Lake, and Lake Louise. Parkland (Wailes & Tiffany 1929).

Alpine France and Norway (Allorge, Ström).

*STAURASTRUM MUTICUM* Bréb.

Alpine moss beds, Bald Mts. Parkland (Wailes & Tiffany 1929).

*STAURASTRUM NATATOR* West var. *RHOMBOIDEUM*, nov. (cf. Wailes, 1932, figs. 12 & 13, p. 23).

Alpine lakes, pools, rivulets, and moss beds, Bald Mts., and Eagle Pass. Parkland (Wailes 1932).

Cellulis e latere visis cum processibus fere duplo latoribus quam longis; semicellulis obverse subsemicircularibus, apicibus subconvexis aut ferme rectis, singulis verrucis v. spinis 3 instructis; processibus brevibus crassis horizontaliter porrectis v. leniter convergentibus, seriebus granulorum 3 concentricis atque ad apices spinis 3 aut 4 instructis; fundo semicellularum circulo granulorum ad sinum praedito: e vertice visis rhomboidalibus, tumore et processibus brevibus crassis fere aequo modo extensis; cetera ut in forma typica.

L. about 30–40  $\mu$ ; B. about 40–50  $\mu$ ; B. of isthmus about 14  $\mu$ .

Forma *TRIQUETRA* (cf. Wailes, 1930 *b*, fig. 28, p. 163). (Figs. 33, 34.)

Common in parkland, moss beds, or in alpine lakes, Eagle Pass.

*S. natator* var. *rhomboidum*, which I have seen from various localities in the United States, is a very beautiful alga. The figures of Wailes, published without a name, which are cited above, probably refer to this form. It differs from the type in the more fusiform shape of the semicell and the shorter stout processes which are nearly straight, and also in its larger tumours. In the latter character it resembles var. *crassum* West, though it is very different in other respects.

\**STAURASTRUM ORBICULARE* Ralfs var. *EXTENSUM* Nordst.

Alpine pools. Field and Quartz Creek.

\**STAURASTRUM PACHYRHYNCHUM* Nordst.

Alpine pools and moss beds, Bald Mts.

*STAURASTRUM POLYMORPHUM* Bréb.

Amongst mosses, alpine spring, Bald Mts. Lowland (Wailes 1930 *a*).

Alpine France and Norway (Allorge, Deflandre, Ström).

\**STAURASTRUM PUNCTULATUM* Bréb. var. *KJELLMANI* Wille

Alpine or parkland, lakes, pools, rivulets, moss beds, or wet rocks, Bald Mts. and Glacier.

\**STAURASTRUM SCABRUM* Bréb.

Alpine pools and quiet ditches, Quartz Creek.

*STAURASTRUM SEXCOSTATUM* Bréb. var. *PRODUCTUM* West

Alpine pools and moss beds, Bald Mts. Parkland (Wailes & Tiffany 1929).

\**STAURASTRUM SPONGIOSUM* Bréb.

Alpine pools, lakes, quiet ditches, or moss beds, Bald Mts.

Recorded from alpine France and Norway (Allorge, Deflandre, Ström).

\**STAURASTRUM TETRAEERUM* Ralfs forma *TRIGONA*.

Alpine pools, Bald Mts.

*EUASTRIDIDIUM* West\**EUASTRIDIDIUM VERRUCOSUM*, sp. n. (Figs. 29, 30.)

Alpine moss beds, Bald Mts. and Glacier.

*Eu. parvum*,  $1\frac{1}{2}$ -plo longius quam latum, profundiuscule constrictum, sinu aperto et rectangulari; semicellulis e latere visis rotundatis circulo processum breviorum 8 circa partem latissimam praeditis, et ad apicem 4; processibus seriebus concentricis verrucarum instructis: e vertice visis globosis, ad marginem processibus 8, centrum versus 4 praeditis.

L. about 48  $\mu$ ; B. about 35  $\mu$  (including the processes); isthmus, about 15  $\mu$ .

There is one axile chloroplast in each semicell with a central pyrenoid and lobes radiating into each process.

This desmid is different from the two species of the genus previously described. From *E. staurastroides* Carter (1926) it differs in the shape of the semicells and the form of the sinus. It resembles *E. Prainii* West (1907) in some respects, but is smaller and has much more prolonged processes. Moreover, the granulation is different.

It has been suggested by Grönblad (1931) that the genus *Euastridium* should be abolished, and that *E. Prainii* should be renamed *Staurastrum Euastridium* (West) Grönblad. The genus *Euastridium* was founded by W. & G. S. West on the basis of its resemblance to *Euastrum* in the general shape of its cell in the front view and the radial symmetry of the vertical view. The similarity to *Staurastrum* was pointed out by the authors (1907, p. 200). *Euastridium staurastroides* from Assam, the second species to be discovered, is even more reminiscent of *Euastrum* than is *Euastridium Prainii*. In the vertical view, however, it is three-lobed, and like *E. Prainii* it has twice as many lobes at the greatest width of the semicell as at the apex. In *E. verrucosum* the general characters are those of *E. Prainii*, with the lobes more produced, emphasising still more the resemblance to *Staurastrum*. That Grönblad is correct in pointing out the close relationship between *Euastridium* and *Staurastrum* cannot be denied, and there is perhaps some justification for his suggestion that *Euastridium* should be abolished. There are several small distinctions, however, which seem to characterize *Euastridium*, though it may be objected that these scarcely warrant the separation of *Euastridium* as a genus:—(1) The peculiar symmetry of the vertical view, which shows twice as many lobes at the widest part of the semicell as compared with the apex. Most *Staurastrum* species of similar form, such as *S. Tohopecaligense* Wolle, *S. furcatum* (Ehr.) Bréb. and *S. arctiscon* (Ehr.) Lund. have the greater number of processes on the apex. This point is, of course, open to the objection that variation in the number of processes is not uncommon in *Staurastrum*. (2) The verrucose nature of the cell-wall common to all three species of *Euastridium* is not frequent in *Staurastrum*.

Grönblad (1931) has pointed out that there is great resemblance between *Euastridium Prainii* and *Staurastrum polonicum* Racib. in Dick (1923). This form seems to have the same symmetry as *Euastridium Prainii*, but the number of lobes is variable, as Dick (1923, pl. ii, f. 9) figures an individual with seven at the lower angles and four at the upper angles. Possibly *Staurastrum polonicum* could be considered as a small form of *Euastridium Prainii*.

The discovery of *E. verrucosum* certainly strengthens the link with *Staurastrum*, yet the three species of *Euastridium* now known seem to have certain characters which isolate them from *Staurastrum*. One must remember also that the limits between other genera of desmids are by no means sharply defined, as it proved by the existence of triradiate forms of *Cosmarium* and biradiate forms of *Staurastrum*. In spite of these links, however, it is found convenient to retain the different genera, and future experience will show whether it is better to retain the genus *Euastridium* or whether it is wiser to include it in the genus *Staurastrum*.

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Studies in Floral Anatomy.—II. The floral anatomy of *Glaucium flavum* with reference to other members of the Papaveraceae. By JEAN DICKSON, B.Sc. (Communicated by Dr. HELEN BANCROFT, F.L.S.)

(With 31 Text-figures)

[Read 25 October 1934]

### I. DESCRIPTION OF TYPES.

#### 1. *GLAUCIUM FLAVUM* Cr.

*Glaucium flavum* Cr., the Yellow Horned Poppy, is a perennial or biennial herbaceous plant of the sea-coast, and is a native of Britain.

The golden yellow flowers occur singly in the axil of a leaf-like bract; the two green hairy sepals are shed as soon as the four petals begin to expand. In a flower-bud the edges of the sepals overlap alternately and the innermost edge of each sepal has a wide membranous margin. Although the petals are distinctly in two whorls, an outer and an inner (as will be seen from the anatomical description), in the bud or half-open flower the margins of the petals overlap one another in the same way as the sepals (i.e. in an imbricate manner).

The numerous stamens have long yellow filaments and orange anthers; they are clustered round the green horn-shaped fruit in a pyramidal manner with a two-grouped appearance. The receptacle, however, is almost flat, and the raising of the anthers to different levels is due to the varying length of the filaments.

The gynaecium is elongated and slender, with two well-defined ribs, and is crowned by a large bi-lobed stigma (fig. 1, a, b).

In an open flower of *Glaucium flavum* the gynaecium projects a little way beyond the stamens, but after fertilization has taken place and when the petals and stamens have been shed the size of the gynaecium increases very rapidly and a ripe fruit often attains the length of 12 inches.

The number of main vascular bundles in the floral axis of *Glaucium flavum* varies from eight to typically twelve; in most of the specimens which were examined there were numerous small strands accompanying them. In the typical cases, with twelve main axial bundles, six of these supply each of the two sepals. The components of the central vascular stele fuse as each of the twelve bundles sends out two branches, so that primarily a sepal has twelve vascular strands; these divide repeatedly as the organ develops and increases in width (fig. 2, a-d, ss.).

When the sepal-supplies have left the central column, there remains a rough circle of vascular tissue in the floral axis. The circle, which is seldom perfect



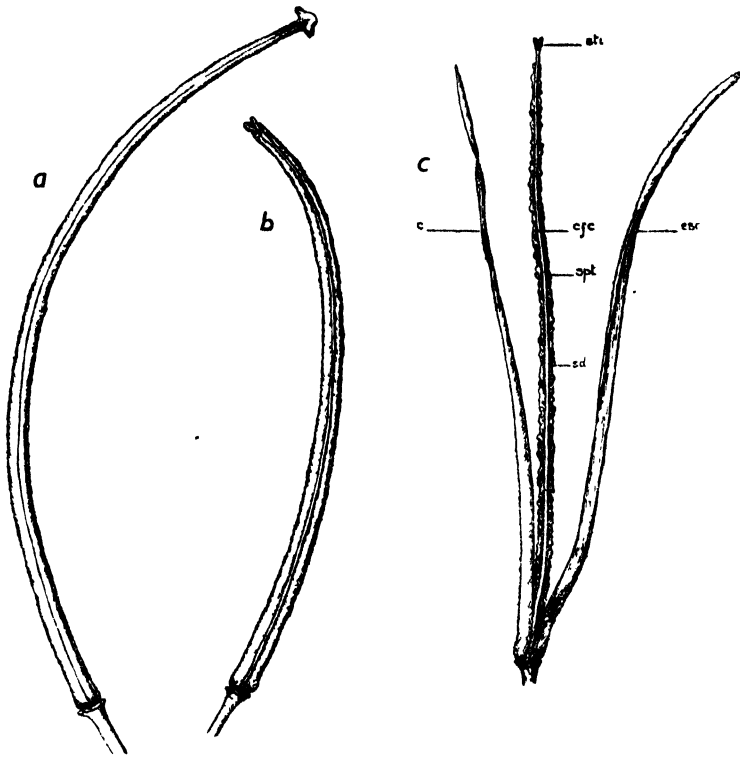


FIG. 1.—*Glaucium flavum* Cr. *a* & *b*. Entire fruit showing position of the stigmatic lobes. *c*. Expanded sterile carpels (*esc.*) splitting away as valves, contracted fertile carpels (*efc.*) with fully developed 'spongy tissue' (*spt.*) in which seeds (*sd.*) are embedded. ( $\times \frac{1}{2}$ .)

FIG. 2.—*Glaucium flavum* Cr.

- a*. T. S. through the base of the receptacle, showing typical arrangement and number of vascular strands.
- b*. T. S. through the base of one sepal, showing the derivation of sepal-supplies (*ss.*) from primary strands of the axis.
- c*. T. S. showing partial separation of one sepal (*s.*), strands for the second sepal (*ss.*), and petal strands (*ps.*), also two of the four vascular groups (*sts.*+*gs.*) from which the stamen-supplies arise.
- d, e*. T. S. showing four vascular groups supplying the stamens (*sts.*+*gs.*), also stamen strands breaking up and taking their positions in the stamen bases.
- f*. The amalgamation of the strands, after the staminal series have become defined, into two definite carpellary whorls, i.e. supplies to two (outer) expanded sterile carpels (*escs.*) and two (inner) contracted fertile carpels (*efcs.*)  
(Note the one-sided development of the bud.)
- g, h, i*. Formation of the gynaecium.  
(Note the absence of ovules.)
- j-m*. Formation of the stigmas; sections show the dividing of the contracted fertile carpel strands to provide each lobe with  $\frac{1}{2} + 1 + \frac{1}{2}$  strands.  
(*a-h*,  $\times 15$ ; *i-m*,  $\times 35$ .)

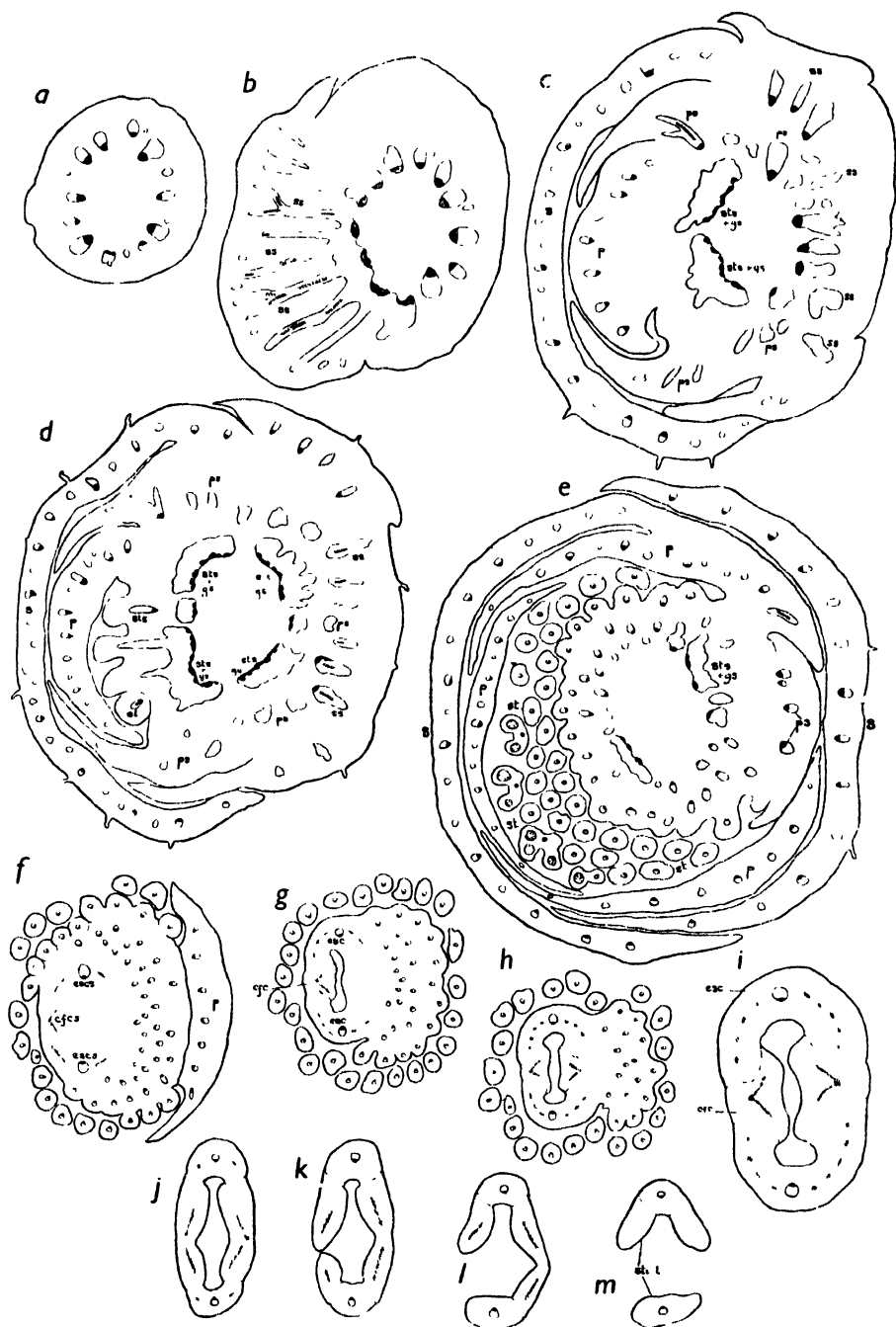


FIG. 2.

owing to the one-sided growth of the bud, is divided into four parts by the separation of the petal-supplies, which move from the centre in alternating pairs, thus forming the two petal whorls. The primary supply to each petal consists of three bundles, which branch many times during the growth of the limb (fig. 2, c, d, *ps.*).

The petals having been accounted for, there remain in the centre of the flower four outstanding groups of vascular tissue which contain the supplies for the stamens and also for the gynaecium (fig. 2, d, e, *sts.* + *gs.*). The number of stamens varies considerably in each individual; specimens examined had 90, 94, 105, 110, 111, 116, 121, or 134, giving an approximate average of 110 to each flower; the whole androecium arises in from four to six irregularly alternating whorls. The supplies to the stamens arise from the four vascular groups, but there is no indication of a four-grouped arrangement when the stamens are free from the axis (fig. 2, e).

The number and arrangement of the staminal series in the Papaveraceae, and especially in the subfamily Papaveroideae, are difficult points to determine, and considerable variation is found from flower to flower in genera and species; there seems to be no definite solution to the question of staminal arrangement in *Glauadium flavum* Cr.

When the staminal whorls have been completed, there remains in the centre of the flower-axis a mass of vascular tissue comprising the gynaecium strands. These aggregate into four groups, which rapidly assume a two-paired arrangement, one pair lying slightly within the other (fig. 2, f-i). The two outer groups supply two large carpels, which lie opposite the outer petals and which almost completely enclose two smaller carpels, each supplied by an inner group of vascular strands. The contracted inner carpels are fertile, producing ovules at their margins, while the greatly expanded outer carpels are sterile and function as protectors to the ovules—a condition recalling that in the Crucifer gynaecium as described by Saunders (22) and Eames and Wilson (6, 7)\*.

\* It is necessary to point out that in interpreting the various gynaecia mentioned in this paper that the terms 'sterile valve carpels' and 'fertile solid, or semi-solid, carpels' have been strictly avoided.

Saunders (22), in whose papers the terms originated, would imply by their use that there exist in the gynaecia which exhibit differentiation of carpels two distinct forms—that is to say, 'carpels of different structural types, fulfilling different functions' (22, p. 123); the gynaecium composed of such carpels is thus a 'polymorphic gynaecium'.

I have avoided the use of the term 'polymorphic', for it indicates that there are present in the gynaecium distinct kinds of carpels; whereas on the examination of this particular type of gynaecium it soon becomes apparent that the carpels are *structurally* similar in their origin and that the narrow ribs of such a gynaecium are only 'an extreme modification of a normal carpel' (7, p. 369).

The degrees of contraction of the fertile carpels here shown are steps in the evolution of the type of gynaecium found in the Rhoeadales, for it is possible to trace the gradual contraction of a carpel, with its vascular anatomy, from a comparatively wide rib to a very fine one.

'Valve carpels' in the Rhoeadales are not always sterile, for, as will be shown in

Each expanded carpel has one main vascular strand which remains constant and several or more lateral veins on either side which vary in size at different levels. At an early stage the fertile carpels have from five to eight strands each, all more or less the same size, but as the gynaecium develops the strands converge so that the numbers in the fertile carpels of an open flower are usually from three to five.

The gynaecium in *Glaucium flavum* is surmounted by a large compound stigma with two lobes which are roughly triangular in shape, the apex of the triangle in each being situated immediately over the midrib of an expanded carpel (fig. 3, a, b). The vascular supplies to each lobe actually consist of the

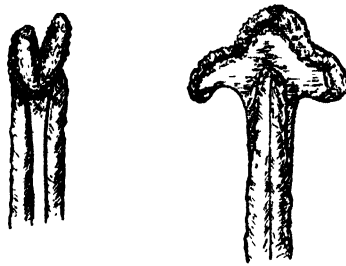


FIG. 3.—Stigmas of *Glaucium flavum* Cr. Drawing to show the position of apices of the stigmatic lobes, i.e. over the midribs of the expanded sterile carpels. ( $\times 2$ .)

strands of one expanded carpel *plus* half the strands of each of the fertile contracted carpels (fig. 2, i-m).

The gynaecium appears to develop very slowly until after fertilization has taken place. Although the vascular supplies are in position, they contain little or no xylem and there is only a slight indication of the points of fusion between the four carpels. The kidney-shaped ovules are peculiar in their late

*Platystigma*, for example, the carpels are to be regarded as normal fused fertile 'valves'.

It is essential that terms be found which at once indicate that there is no *fundamental* difference between the two carpel conditions; therefore throughout the descriptions in this paper the 'valves' are referred to as expanded carpels, either fertile or sterile, as the case may be, and the 'solid carpels' as contracted carpels.

Among the carpels in the last-mentioned condition are found many degrees of contraction ranging from moderately wide ribs with an indefinite number of vascular strands, as in *Glaucium* and *Sanguinaria*, to extremely narrow ones with the vascular strands contracted to a single cord, as in *Helidonium*. But the constant feature in this condition of carpel (at any rate, in the types here examined) is that they are always fertile, whereas expanded carpels may be either fertile or sterile.

No gynaecium amongst those examined was made up entirely of contracted carpels, but a gynaecium which showed differentiation of carpels never exhibited *fertile* expanded carpels. The fertile expanded carpels were found only in those gynaecia which showed no differentiation of carpel conditions, e.g. *Platystemon*, *Platystigma*, and *Romneya* (Papaveraceae); similar types of gynaecia also occur, for example, in *Aquilegia* (Ranunculaceae) and *Reseda* (Resedaceae).

development. Sections cut from specimens of *Glaucium* buds of varying length showed that, while the flower was complete in all its other parts, the ovules were absent. This proved to be so until the ovary has grown to about 1 cm. in length.

In young gynaecea (i.e. from 1 cm. to 3 cm. in length) the ovules project from the placentae on the fertile carpels into the loculi formed by the sterile carpels (fig. 4).

After fertilization and when the fruits have grown to about 3 cm. in length a soft sponge-like tissue develops from the inner margins of the contracted carpels and extends into the ovary cavity (fig. 2, c). Ultimately, in fruits of 9 cm. and upwards, the ovary is divided into two parts by the fusion of this 'spongy' tissue to form a false septum. In its growth the septal tissue

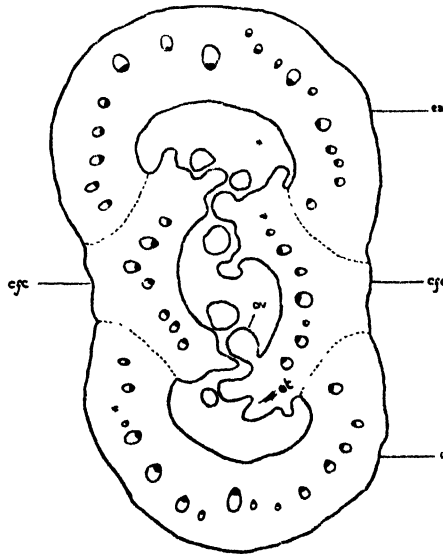


FIG. 4.—*Glaucium flavum* Cr. Production of ovules in an older specimen. *ov.*, ovule; *ot.*, ovule trace; *esc.*, expanded sterile carpel; *cfc.*, contracted fertile carpel. ( $\times 15$ .)

penetrates between the seeds, partially or, sometimes entirely, surrounding and embedding them; the rate of development of this false septum varies to some extent in each individual.

When the fruit is ripe, the expanded carpels split off as valves from the fertile carpels from the top downwards; in so doing, they bend outwards, leaving the fertile carpels standing erect, crowned by the stigmas and connected throughout their length by the false septum with its embedded seeds. The expanded 'valves' do not fall off entirely, but remain attached to the receptacle. The 'spongy' tissue ultimately dries and shrinks so that the seeds fall to the ground; the tissue itself tends to break away from the fertile carpels,

leaving these organs standing free from each other, except at the tip, where they are connected by the stigmas which always remain intact. The apparent use of the 'spongy' tissue is to carry and protect the seeds when the expanded carpels become detached from the contracted carpels. In *Glaucium flavum*, if the tissue were not present, the seeds would easily become detached from the placentae before they were ripe, as they are not shed immediately the capsule splits.

## 2. *PLATYSTEMON CALIFORNICUS* Benth.

*Platystemon californicus* Benth. belongs to the group in the Papaveraceae which is characterized by having three sepals and six petals, the latter being arranged in two whorls of three in this genus.

The androecium consists of numerous pale yellow stamens with long extrorse anthers and flexible flat filaments; the stamens are clustered round the



FIG. 5.—Fruit of *Platystemon californicus* Benth. ( $\times 2$ .)

gynaeceum which is strongly ribbed, each rib being terminated by a slender stigma (fig. 5).

The normal number of vascular strands in the slender peduncle of *Platystemon californicus* is six, but specimens were found in which five of the bundles were well developed, while the sixth was considerably reduced in size\*. The bundles are large in proportion to the size of the stem and contain strongly defined xylem elements.

The six vascular bundles in the floral axis of *Platystemon californicus* are alternately large and small (fig. 6, a), and in the formation of the sepal strands each of the three larger bundles provides a strong strand which takes up the position as the midrib of a sepal. Each of the three smaller strands in the axis

\* One flower which had only five strands in the peduncle also had only five petals.

gives rise to two branches which move out to form the lateral veins of two neighbouring sepals; thus each sepal has primarily the  $\frac{1}{2}+1+\frac{1}{2}$  bundle formation (fig. 6, b-d).

The residual vascular tissue now lying in the axis consists of six bundles which are arranged in two whorls of three; the outer whorl supplies the outer petals which alternate with the sepals, and the inner whorl supplies the inner petals which lie opposite to the sepals (fig. 6, c, d, *ps.*, *p.*). In the central vascular ring there is one bundle allotted to each petal, but when these bundles begin to move out in order to take up their positions in the petal-bases they undergo certain changes.

As the three bundles which supply the outer whorl of petals leave the stele, they divide radially into three parts (sometimes only two), and each part behaves in the same way as the single bundles which supply the inner (smaller) petals (fig. 6, c, d, *ps.*). These bundles move from the stele as one strand, but branch into three before they enter the bases of the petals.

Alternating with the petals there now remain in the axis six masses of vascular tissue which become broken up as they provide the numerous stamens with their vascular elements (fig. 6, d, *sts.*+*gs.*), and here again, as in *Glaucium flavum*, the gynaecium supplies cannot be distinguished in the central mass until the stamens have become differentiated.

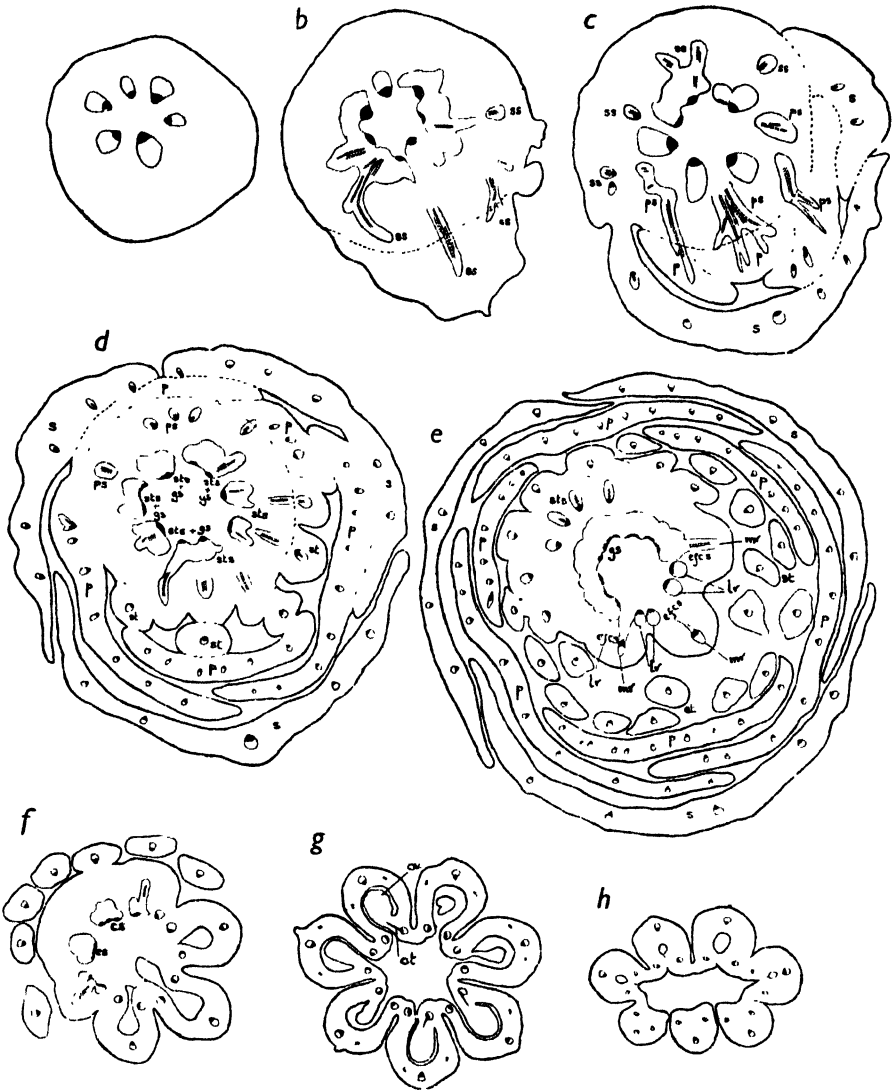
The androecium arises in irregular alternating series, which vary according to the number of stamens and the size of the flower (fig. 6, e).

When the staminal whorls have been completed, there remain in the floral axis a number of vascular groups, fused more or less into a cylinder, which comprise the supplies to the carpels (fig. 6, e, *gs.*). Externally the gynaecium of *Platystemon* appears to be made up of an indefinite number of normally formed carpels which are lightly fused with one another, and an examination of serial sections proves this to be correct.

Each of the vascular groups represents the supplies to a single carpel (therefore the number of groups varies in each flower), and provides it with a midrib and two lateral strands in the normal manner, that is to say, the midrib moves out first from the vascular cylinder and takes up its ultimate position in the carpel-wall, which by this time has begun to become differentiated from the receptacle (fig. 6, e, *mr.*). At a slightly higher level the two lateral strands leave the axis and assume their positions in the margins of the carpels (fig. 6, e, f, *lr.*).

The inner faces of the margins bear the placentae, and these are never fused with each other, but lie in close contact. This accounts for the finding sometimes of an ovule, which has, owing to spacing difficulties, become extruded from the cavity of an individual carpel and is lying in the central cavity of the gynaecium as a whole (fig. 7, *eo.*).

At the top of the gynaecium the carpels separate from one another and become much narrower. The cavities become closed over by the formation of the stigmas (one to each carpel), but the central cavity of the gynaecium as

FIG. 6.—*Platystemon californicus* Benth.

- a. T. S. through the base of the receptacle.
- b, c. T. S. showing sepal strands (*ss.*), bases of sepals (*s.*), derivation of the petal strands (*ps.*) and the bases of the petals (*p.*).
- d. T. S. showing sepals (*s.*), petals (*p.*), derivation of staminal supplies (*sts.*) from central masses of vascular tissue, which consist of stamen and gynaecium strands (*sts.* + *gs.*).
- e. Showing extreme base of three carpels (*efcs.*) with midrib (*mr.*) and laterals (*lr.*) taking up their positions.
- f-h. Stages in the development of gynaecium; carpel supplies (*cs.*), lateral ribs (*lr.*), mid-ribs (*mr.*), expanded fertile carpel (*efc.*), ovule (*ov.*), ovule trace (*ot.*), arising from lateral strand of carpel and contraction of carpels to form stigmas. ( $\times 35$ .)



a whole remains unchanged. As the individual carpel narrows, the subsidiary strands die out; the lateral ribs become much weaker and eventually fuse with the midrib which always provides the solitary vascular strand of the stigma.

When the gynaecium is ripe, the dispersal of seeds occurs in a way that is unusual in the follicular fruit. As the various carpels or 'follicles' mature they become divided transversely into several one-seeded segments by a thickening of the carpel-wall towards the centre of the cavity. The seeds increase in size and cause the segments to swell, so that each 'follicle' has a torulose appearance similar to that of a *Raphanus* (Cruciferae) fruit. The 'follicles' then separate longitudinally from each other, and finally break up into numerous one-seeded portions.

Thus, during their life-history, the fruits of *Platystemon californicus* present three different types: firstly, a vertically ribbed capsule; secondly, an

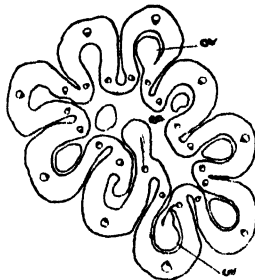


FIG. 7.—T. S. gynaecium of *Platystemon californicus* Benth., showing ovules in normal position in individual carpels (*ov.*) and ovules expelled into the cavity of the gynaecium as a whole (*eo.*). ( $\times 35$ .)

etaerio of 'follicles'; and, thirdly, when seed dispersal takes place, a collection of schizocarpic fruits.

*Platystemon* therefore exhibits, in these features, characters which are not found in any other Papaveraceous type, and this genus of the Papaveraceae appears to be the only one in which the seeds are shed while still enclosed in a part of the ovary.

### 3. PLATYSTIGMA OREGANUM Benth. & Hook. fil. (*Meconella oregana* Nutt.).

(NOTE.—The description of this plant is unfortunately incomplete, owing to the difficulty in obtaining material for microscopic examination. It was not possible to get fresh specimens and only the gynaecia of the herbarium material were suitable for sectioning.)

The vascular stele at the base of the ovary consists of nine small bundles (which sometimes show a tendency to fuse with each other), arranged in a circle. From this circle three strands move out, leaving in the centre of the axis three pairs of bundles (fig. 8, a).

The three strands which depart first from the stele are the midribs of the three normal expanded fertile carpels which constitute the gynaecium. (Rarely there are four carpels.)

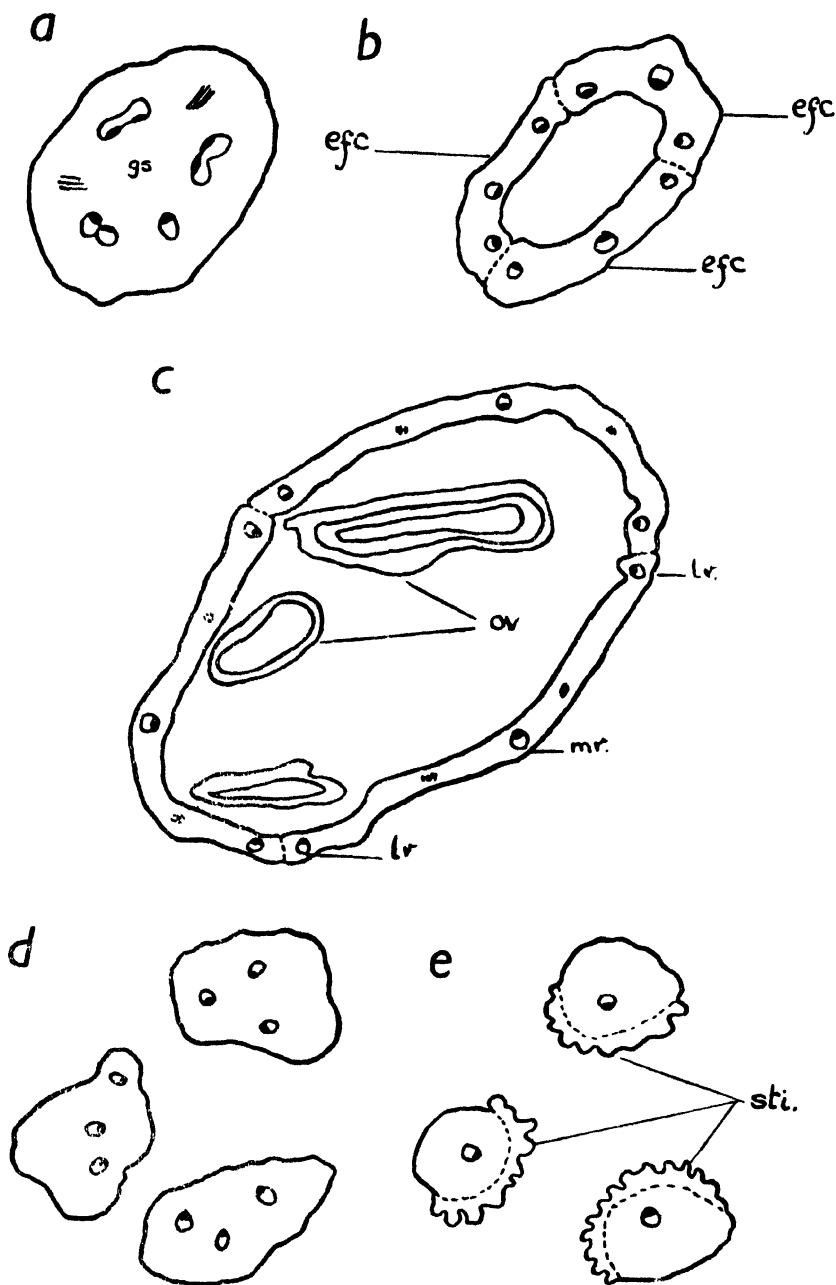


FIG. 8.—*Platystigma oreganum* Benth. & Hook. fil.

- a. Base of gynaecium showing vascular supplies (*gs.*).  
 b. Gynaecium strands taking up their ultimate positions. *efc.*, expanded fertile carpol.  
 c. Three carpels with midrib (*mr.*), lateral ribs (*lr.*), and ovules which are produced on the margins of the carpels (*ov.*).  
 d, e. Formation of stigmata (*sti.*). ( $\times 70.$ )

While the midribs take up their position, the remaining strands move outwards and each pair of strands is to be regarded as composed of a lateral vein from each of two adjoining carpels (fig. 8, b, c). By this time the central loculus of the gynaeceum has begun to open out, and it will be seen that each normal expanded fertile carpel has at this level three well-marked vascular



FIG. 9.—Fruit of *Platystigma oreganum* Benth. & Hook. fil., showing position of stigmas. ( $\times 2$ .)

strands. As the gynaeceum increases in circumference, very small subsidiary strands appear between the midribs and the lateral strands. The ovules are produced in the normal position on the fused margins of the carpels, their vascular supplies being derived from the lateral strands (fig. 8, c).

When the ovary begins to taper on nearing the apex, the subsidiary strands die out and the main vascular strands of each carpel draw together and finally become united into a single cord. It is this cord which provides the vascular supply to the blunt stigmatic lobe which surmounts the carpel (fig. 8, d, e).



FIG. 10.—Fruit of *Romneya Coulteri* Harv. (Nat. size)

#### 4. ROMNEYA COULTERI Harv.

(NOTE.—Owing to unfavourable material, it was impossible to obtain a perfect series of sections through the whole flower. The calyx, corolla, and androecium were destroyed, but it was possible to make a fairly detailed examination of the

gynaeceum, although serial sections were difficult to obtain owing to the hard and bristly external layer of the ovary wall.)

The gynaeceum of *Romneya Coulteri* Harv. is an ovoid structure, covered with stiff adpressed bristles and surmounted by a cluster of blunt stigmatic lobes. The vascular anatomy is somewhat complicated, and, owing to the size of the gynaeceum, presents a certain amount of variation.

After the departure of the vascular supplies to the perianth segments and androecium (which apparently behave in a very similar manner to those of *Papaver*), the residual strands form a ring in the centre of the floral receptacle.

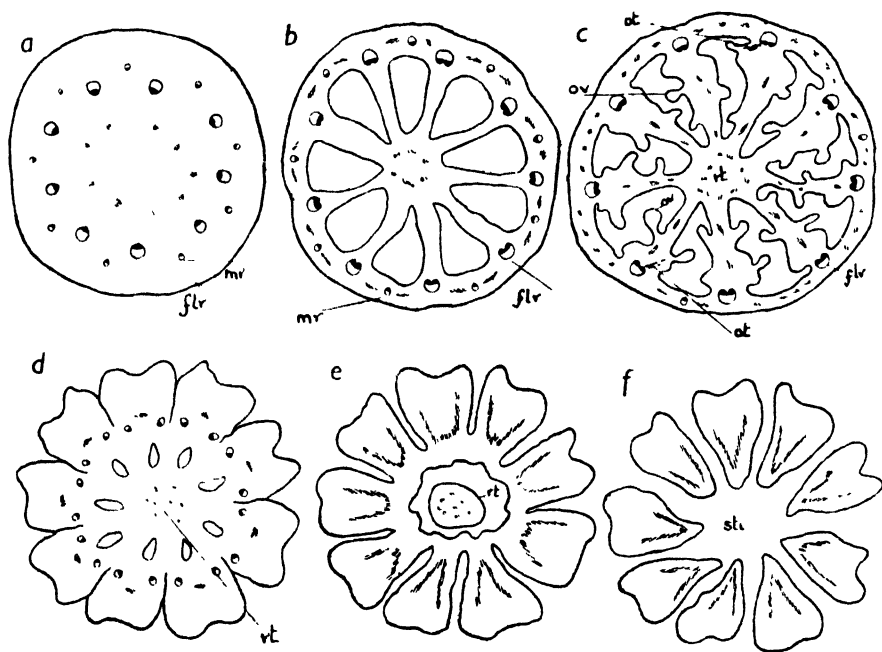


FIG. 11.—*Romneya Coulteri* Harv.

- a. T. S. of ovary base showing fused lateral ribs (*flr.*) and midribs (*mr.*).
- b, c. T. S. showing placentae united with core of residual tissue (*rt.*), ovules (*ov.*), and ovule traces (*ot.*) arising from the fused lateral ribs (*flr.*).
- d. Fused laterals separating from each other.
- e, f. Formation of stigmata, placentae separated from residual tissue (*rt.*), which ultimately disappears. ( $\times 15$  approx.)

From this ring at definite points, which vary according to the number of carpels, weak strands move out and ultimately form the midribs of the carpels. Alternating with these strands there now arises a corresponding number of large composite bundles which are apparently the fused lateral veins of adjoining carpels (fig. 11, a-c). Therefore the gynaeceum consists of numerous fertile expanded carpels fused margin by margin.

In the central cavity of the gynaecium there is a structure which is peculiar to this genus in the Papaveraceae, namely, a persistent central core of receptacular tissue. From the fused carpel margins large placentae, consisting of a mass of loosely-formed tissue, are developed, and these project into the ovary-cavity where they are united with the central core, with the result that a multilocular ovary is formed.

This central core is purely of a residual character, for when the main carpellary supplies have departed from the axis there remain a few weak strands which run up into the core as the ovary develops (fig. 11, b-e).

The core is comparable with the small residual outgrowth of the receptacle which is not infrequently present in the centre of the cluster of free carpels in *Aquilegia* spp. (Ranunculaceae).

Numerous subsidiary vascular strands appear between the three primary strands of each carpel; the ovule-traces arising from the lateral strands run out into the placentae where they are easily to be distinguished. The weak strands in the central core do not play any part in the production of ovule-supplies.

As the stigmatic lobes develop, the central core separates from the placental region and appears as a distinct structure, still bearing very small weak vascular strands, in the centre of a ring of stigmas which are still fused with each other (fig. 11, e).

The stigmas are situated over the midribs of the carpels, and their vascular supplies are derived from both the midribs and the lateral veins; by the time the stigma-lobes are free the central core has tapered away (fig. 11, f).

##### 5. PAPAVER RHOEAS L.

The vascular system in the stem just below the receptacle consists, in the specimen here described, of five large bundles with marked xylem elements and five smaller bundles alternating with them (fig. 12, a).

The main bundles of the axis each give off two branches, so that the total sepal supply consists of ten strands, five of which pass into each sepal (fig. 12, a, b).

After the separation of the sepal strands, the central vascular masses lie in a rough circle, in which, almost immediately, may be distinguished eight main groups of elements (fig. 12, b). The petal strands split off in four groups, each one corresponding to a petal, and each group consisting of several vascular bundles. The petals are thickened at the base, so that the vascular strands do not enter at the point of junction of the petal with the floral axis, but a little higher up. The vascular group breaks up into many small bundles, which then enter the petal, instead of, as in some of the other members of the Papaveraceae, entering the petal as one or several larger strands and then dividing.

Alternating with the petal bundles there remain four residual groups, which contain the vascular supplies of the numerous stamens and of the carpels (fig. 12, c, *sts.* + *gs.*). The stamens appear to be arranged in four irregular

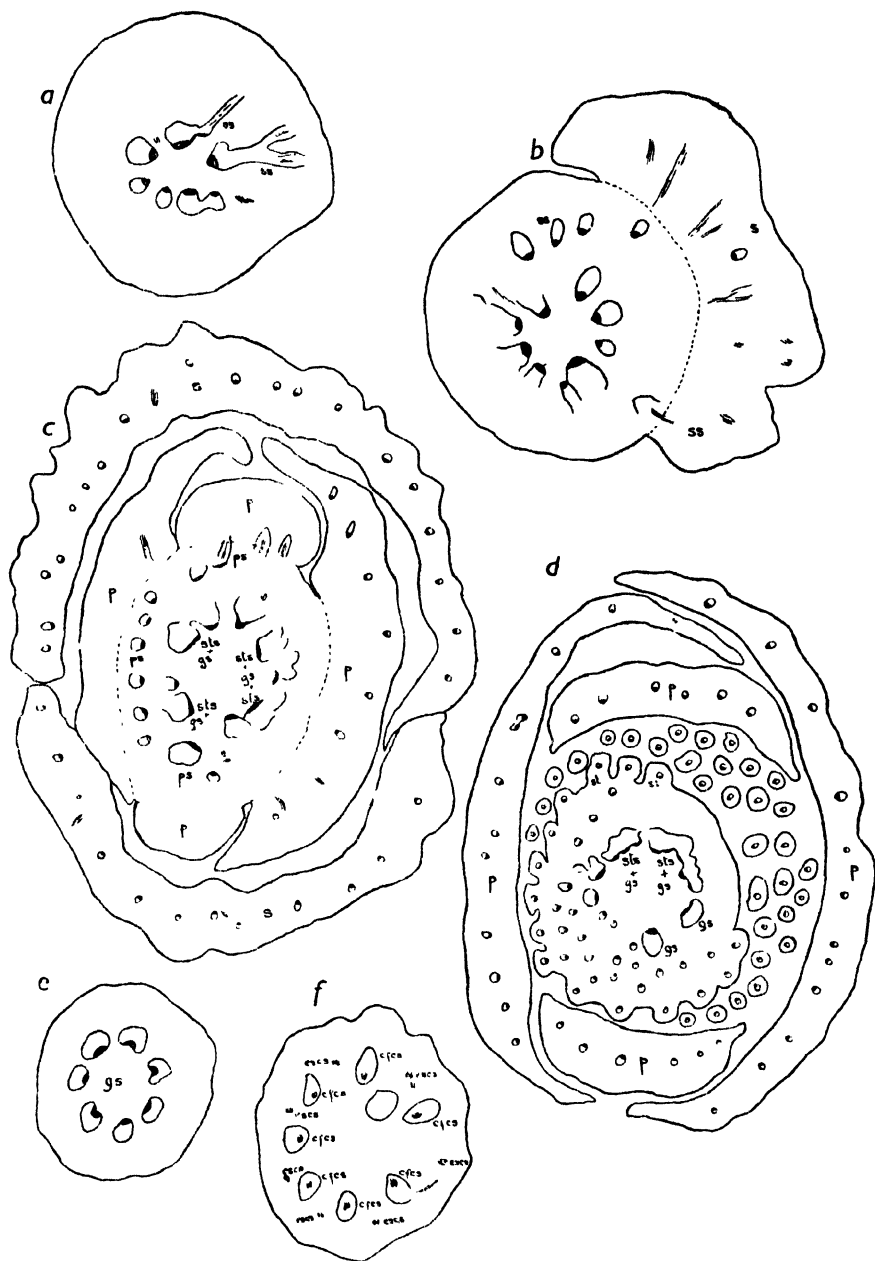


FIG. 12.—*Papaver Rhoeas* L.

- a, b. Derivation of sepal-supplies (ss.) and strands running into sepal base (s.).  
 c. Sepals (s.), bases of petals (p.), petal supplies (ps.), vascular tissue which ultimately provides androecium and gynaecium (sts. + gs.).  
 d. Sepals omitted, petals (p.), staminal whorls becoming differentiated, gynaecium strands (gs.) aggregating in centre.  
 e, f. Primary strands to gynaecium, expanded sterile carpal supplies (escs.), and contracted fertile carpal supplies (cfs.). ( $\times 35$ )

whorls, but no definite statement can be made with regard to the arrangement and number in *Papaver* spp.

The number of vascular strands left after the staminal strands have separated is as variable as the stamens themselves, but the number that remains definitely indicates the number of placental ribs, the bundles supplying which are

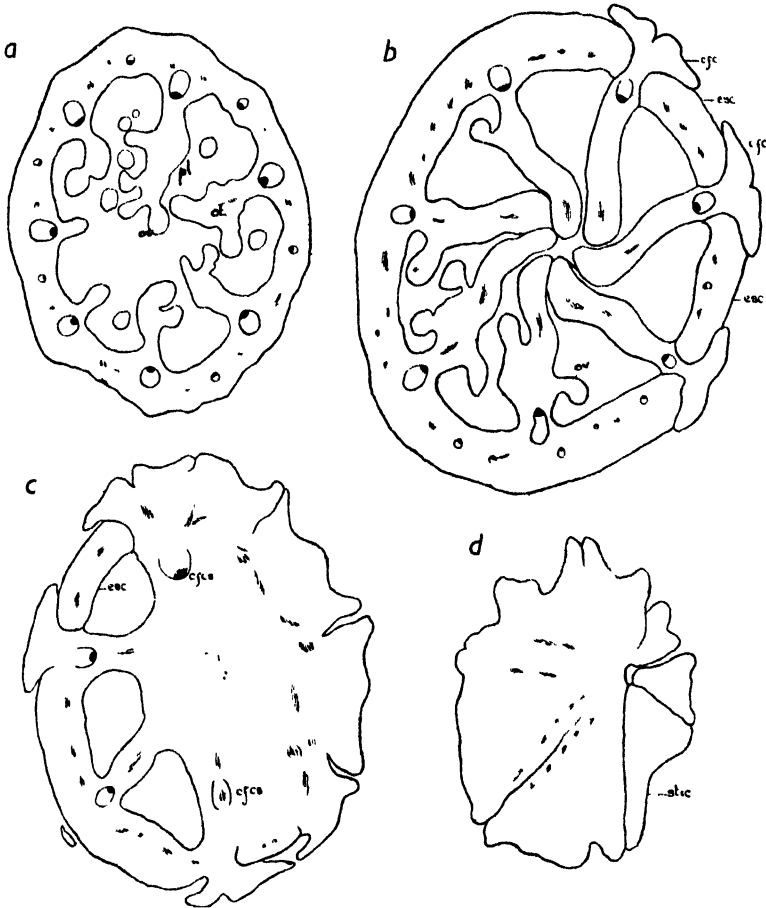


FIG. 13.—*Papaver Rhoeas* L.

- a, b. Ovary increasing in size, with placenta<sup>e</sup> (pl.) projecting towards the centre of cavity.  
 b, c. Expanded sterile carpels tapering just beneath the stigmatic cap.  
 d. Fusion of contracted fertile carpels (cfc.) to form stigmatic cap (stic.). (× 35.)

concentric, the xylem elements tending to be in the centre of a mass of phloem and sclerised tissue ; they move out from the middle of the axis into the ovary-wall, occupying a position opposite to which the placenta<sup>e</sup> ultimately develop. Very weak bundles appear in the wall of the ovary between the large ribs (fig. 12, e, f, cfc<sub>s</sub>., esc<sub>s</sub>.).

The question arises whether there are sterile expanded carpels and contracted fertile carpels in *Papaver* as there are in *Glaucium* etc. Ultimately, this proved to be so, but it is a point which cannot be determined from the examination of ovaries dissected from young buds. The specimen which was used as a basis for this description had seven placental bundles and from one to several smaller bundles in the ovary-walls between the placentae. Whether or not these smaller bundles represented the supplies of expanded carpels could not be ascertained from the young bud. There were no marked lines of junction between the placental bundles and the intervening walls; also both the large placental bundles and the small intervening strands remained in an even ring (fig. 13, a). In the semi-mature capsules of certain other species of *Papaver*, however, the placental ribs occupy a more internal position, while the intervening areas of the compound ovary-wall tend to inclose them, so that the vascular bundles of the gynaeceum as a whole lie in an outer and an inner whorl.

It may therefore be concluded that the sterile areas of the ovary-wall represent expanded sterile carpels comparable with those of *Glaucium*, and that the



FIG. 14.—Capsule of *Papaver* sp., showing pores opening at the apices of the expanded sterile carpels. ( $\times 1\frac{1}{2}$ .)

placental ribs represent the supplies of contracted fertile carpels, also similar to those of *Glaucium*, but exhibiting a greater degree of contraction.

The stigmas are developed entirely from the contracted fertile carpels, which fuse by their margins over the top of the ovary to form a flat, or sometimes conical, cap with a ray of stigmatic papillae in line with each rib (fig. 13, c, d). The edge of the cap, or disk, projects over the tips of the expanded carpels, and in the young fruits is folded against the ovary-wall. Just below the stigmatic cap, the expanded carpels end fairly abruptly, and, when the capsule is ripe, the disk is slightly raised by the prolongation of the placental ribs, and in this way the pores for seed-dispersal are disclosed. *These pores open at tops of the expanded carpels, which are never fused with the stigmatic disk*, for the disk can always be dissected from the capsule without causing any injury to the tips of the expanded carpels. Specimens at every stage of growth were examined, and this was always so in *Papaver Rhoeas*, *P. Argemone*, *P. hybridum*, *P. somniferum*, *P. orientale*, *P. bracteatum*.

The vascular bundles of the contracted carpels remain unchanged throughout their course. When they reach the top of the ovary-wall they bend inwards



almost at right angles and run along underneath the stigmatic rays; the expanded carpels have very weak vascular strands, for though they are fairly well marked at the base of the ovary, they taper considerably towards the top, and great variation in number and size of the strands is to be found in individual cases.

#### 6. *SANGUINARIA CANADENSIS* L.

The vascular system in the stem below the floral axis consists of five groups, two large and three smaller ones, but as in most Papaveraceous types the number of bundles at this point is very variable. The groups appear to be composed of several bundles, for when the strands begin to enlarge at the base of the floral axis each of these groups divides into from two to four portions, according to the size; the resulting bundles ultimately fuse to form a rough circle of vascular tissue with scattered colonies of xylem elements on the inner margins (fig. 15, a).

This vascular ring is again divided into groups by the departure of the strands to the two sepals, and in the particular case here described there are five strands allotted to each sepal (fig. 15, b).

From the remaining portions of the vascular ring there arise, on irregular radii, the large bundles which supply the petals, which in this flower number eight\*. One point is clearly demonstrated by the examination of serial sections of a bud of *Sanguinaria canadensis*, namely, that the petals are formed as individual members of the perianth from the vascular cylinder in the floral axis and are not formed by *dédoublement*, as is suggested by Warming (26) (fig. 15, c, d, *ps.*, *p.*).

When the petals have separated from the receptacle, the residual vascular ring is made up of eight groups, which break up into a number of small strands from which the staminal supplies are derived (fig. 15, d, *sts.* + *gs.*). In the particular flower that is described there are thirty-two stamens which arise from the axis in four irregularly alternating whorls (fig. 15, e, f, *sts.* + *gs.*, *st.*).

After the supplies to the stamens have left the axis, the remnants of the vascular system again unite into a cylinder. This cylinder then divides definitely into four, two large portions alternating with two smaller ones (fig. 16, a).

These portions constitute the primary vascular strands to the gynaecium which is composed of four carpels, two expanded and sterile and two contracted and fertile. As soon as the four vascular groups become differentiated from the stele, the two smaller begin to move out from the centre of the axis and these form the midribs of the expanded carpels; small subsidiary strands also move out to form the lateral veins, but in a young bud these are frequently indistinct (fig. 16, b *et seq.*).

\* Though the petals of *Sanguinaria* may vary in number from eight to twelve, specimens with eight were the most frequent.

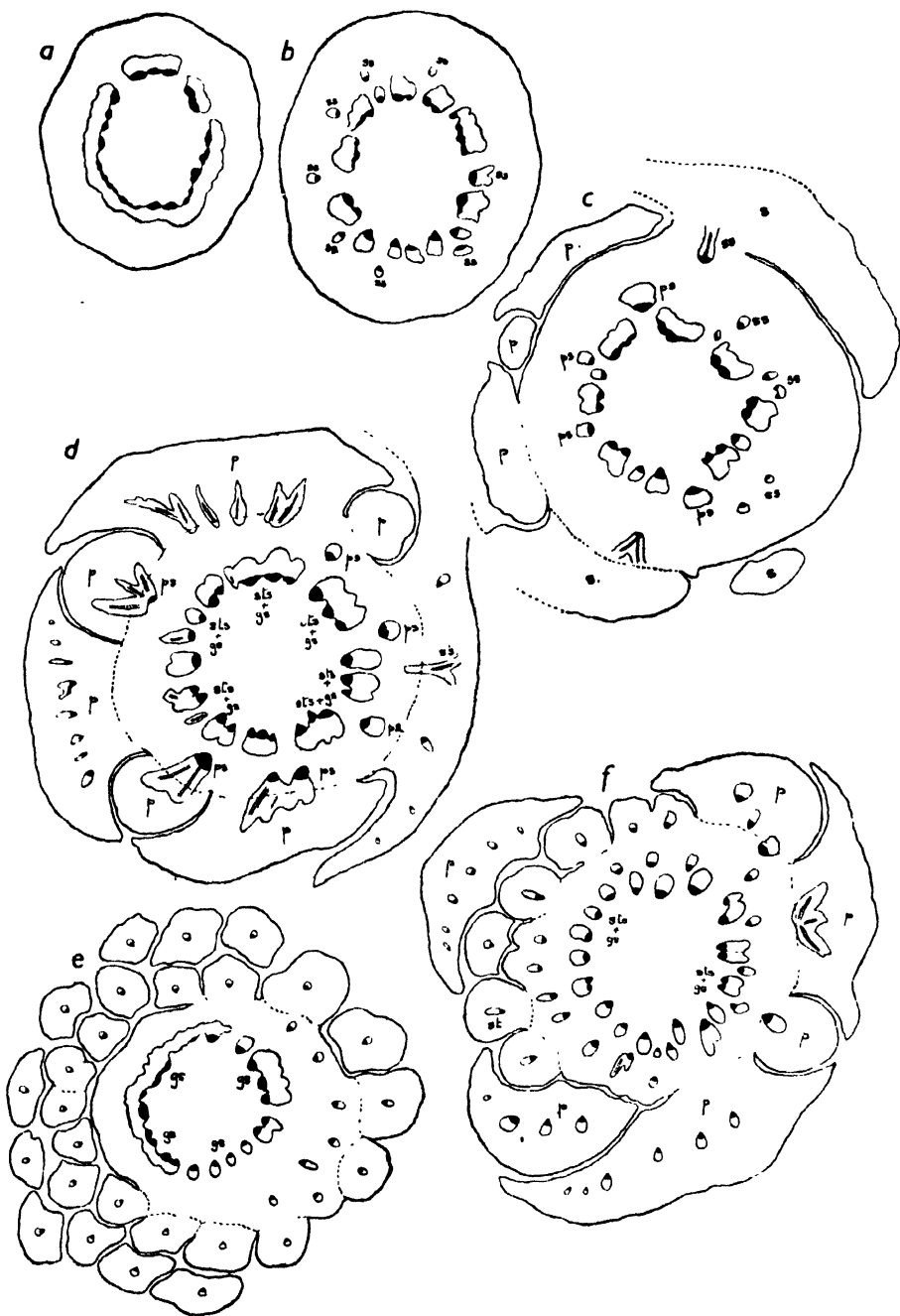


FIG. 15.—*Sanguinaria canadensis* L.

a, b. Derivation of sepal-supplies (ss.) from the receptacular bundles.

c. Sepal-supplies (ss.), bases of sepals (s.), petal-supplies (ps.), and bases of petals (p.).

d, e. Showing vascular tissue from which stamens and gynaecium arise (sts.+gs.).

e, f. Separation of the staminal whorls (st.). (×15.)

The two larger masses of vascular tissue supply the contracted fertile (inner) carpels. The number of strands to each fertile carpel is variable from the outset, for they differ in each individual and at various levels up the gynaecium. The primary strands are frequently from three to five; these may increase or diminish at different levels, but usually they remain fixed at three in the middle and upper portion of the gynaecium (fig. 16, e).

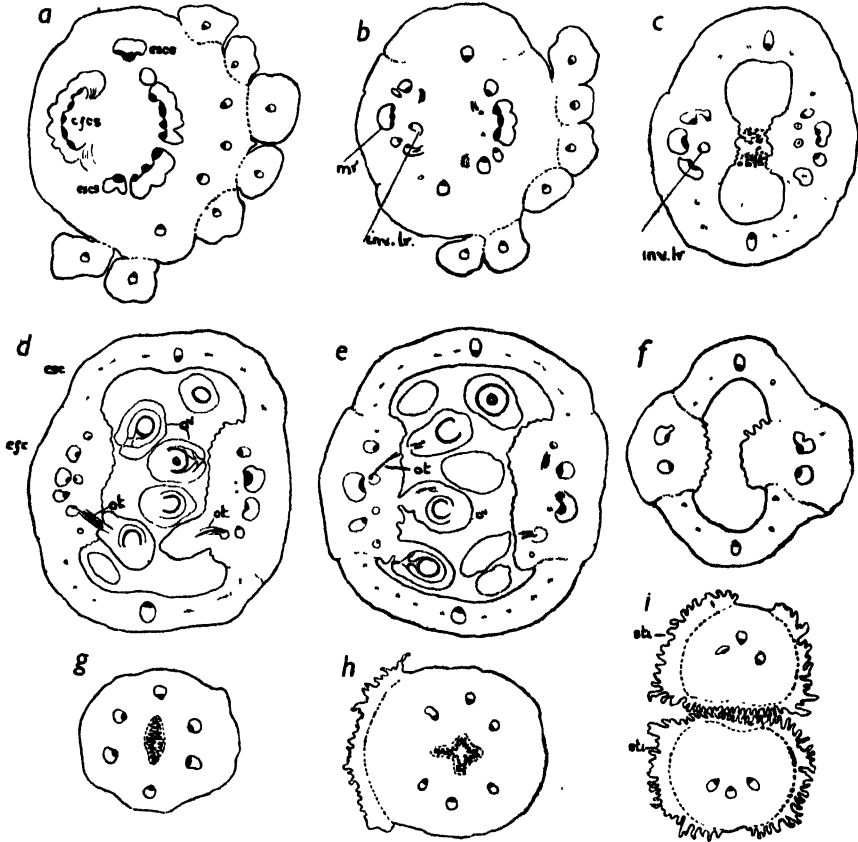


FIG. 16.—*Sanguinaria canadensis* L.

- a, b. Supplies of gynaecium assuming a two-paired arrangement (*escs.*, *cfcs.*). Note particularly the inversion of the lateral strands (*inv.lr.*).  
 c-e. Expansion of gynaecium and derivation of ovule traces (*ot.*) from inverted and non-inverted lateral ribs.  
 f-i. Division of the bundles in contracted fertile carpels, narrowing of gynaecium to form style, and formation of stigmas (*sti.*). ( $\times 15$ .)

In the receptacle the vascular masses allotted to the fertile carpels are crescent-shaped and the 'arms' of the crescent show a tendency to bend inwards towards each other, so that ultimately they lie opposite the midrib of the carpel with the *xylem elements inverted* (fig. 16, a-e).

As the vascular supplies of the ovules are derived from the remaining lateral ribs, and only very rarely from the inverted ribs, it appears that either the entire ventral rib does not change its position, or, owing to the fact that the true ventrals, when inverted, are not in a convenient position and are not developed enough to supply the ovules with a maximum amount of vascular tissue, the function has devolved on another (and more central) pair of laterals; it has already been noted that there are frequently more than three strands in a contracted carpel (fig. 16, d, e).

As the gynaeceum begins to narrow towards the styler region, the vascular strands undergo further changes. The number of strands in a fertile carpel just below this level is three, and as the style is approached the laterals, their function of supplying the ovule-traces having ceased, become very weak and ultimately fuse with the midrib, which, by this time, has divided into two portions in preparation for the formation of the stigmatic lobes (fig. 16, f-i).

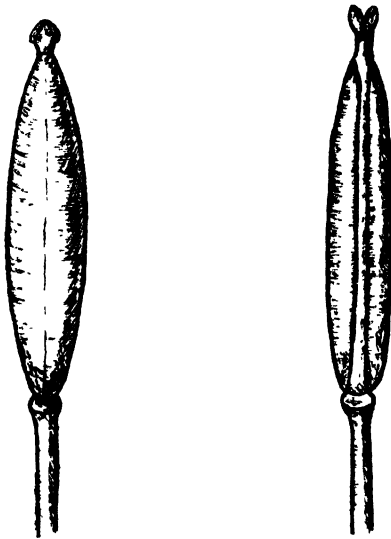


FIG. 17.—Fruits of *Sanguinaria canadensis* L., showing the position of the stigmatic lobes. (Nat. size.)

The midribs of the sterile carpels remain unchanged throughout the entire length of the ovary, but the laterals, like those of the fertile carpels, become very weak and finally die out altogether, so that there are six well-developed vascular bundles in the short style (fig. 16, g). Near the top of the style, half the bundle from each fertile carpel moves out towards the appropriate sterile carpel midrib, so that just beneath the stigmatic lobes there are two opposite groups of vascular tissues consisting of three bundles each (fig. 16, h). There is a cavity running down the centre of the style and the division of the stigmatic region into two parts originates in the wall of this cavity and progresses outwards.

On nearing the apex of the stigmatic lobes, the three strands become considerably smaller and gradually unite into one mass, which, as the lobe tapers, finally disappears altogether.

It has thus been shown that the two large stigmatic lobes of *Sanguinaria* are superposed on the expanded sterile carpels and that in their vascular origin they are the same as those of *Glaucium*—that is to say, they are formed from the strands of  $\frac{1}{2} + 1 + \frac{1}{2}$  carpels.

#### 7. *CHELIDONIUM MAJUS* L.

Each individual flower of *Chelidonium majus* L. is borne on a slender peduncle possessing four vascular bundles, which are large in proportion to the size of the axis. At the extreme base of the floral receptacle these bundles increase in size and show evidence of triple constitution. The three constituents of each group may be united or free, but the four groups themselves remain distinct (fig. 18, a, b).

Each of the two sepals is provided with four main strands which arise from the lateral bundles of the four 'triple' vascular groups in the centre of the axis, two of the groups thus supplying each sepal (fig. 18, c).

The middle bundles of the 'triple' groups remain in the centre of the axis, but gradually become enlarged. Strands depart from both edges of the residual bundles and almost immediately unite in pairs to form the vascular supplies of the four petals (fig. 17, e, f). At the base of the petal the vascular supply consists of one strand, but this at once breaks into three parts on moving up the limb.

Four irregular masses of vascular tissue, which in some cases show a tendency to fuse, are now left in the central stele. The staminal supplies arise from these bundles in what appear to be three whorls of eight (fig. 18, e-h).

The remains of the last four groups, consisting of two large and two small vascular masses, supply the gynaecium, which is made up of an outer whorl of two expanded sterile carpels and an inner whorl of two contracted fertile carpels (fig. 18, f).

The smaller bundles provide the primary vascular supply to each expanded carpel, but as soon as the ovary expands to form a loculus the single bundle splits up into a midrib and two marginal strands (fig. 18, g). These remain unchanged until the top of the capsule is narrowed on the formation of the style, when they diminish in size as the stigmatic lobes develop. In *Chelidonium majus* each lobe of the small bi-lobed stigma is formed over an expanded carpel with the  $\frac{1}{2} + 1 + \frac{1}{2}$  vascular formation, as in *Glaucium* (fig. 17, i-l).

The contracted fertile carpels are supplied by the two larger strands in the axis; each carpel has one concentric vascular bundle, and it seems probable that this is composed of fused strands. As no traces of lateral ribs were found in the contracted carpels, it may perhaps be assumed that the vascular strands in these carpels have undergone a process of contraction similar to that of many members of the Cruciferae. At the extreme base of the gynaecium the contracted carpel-supplies consist of two crescent-shaped vascular masses, and this

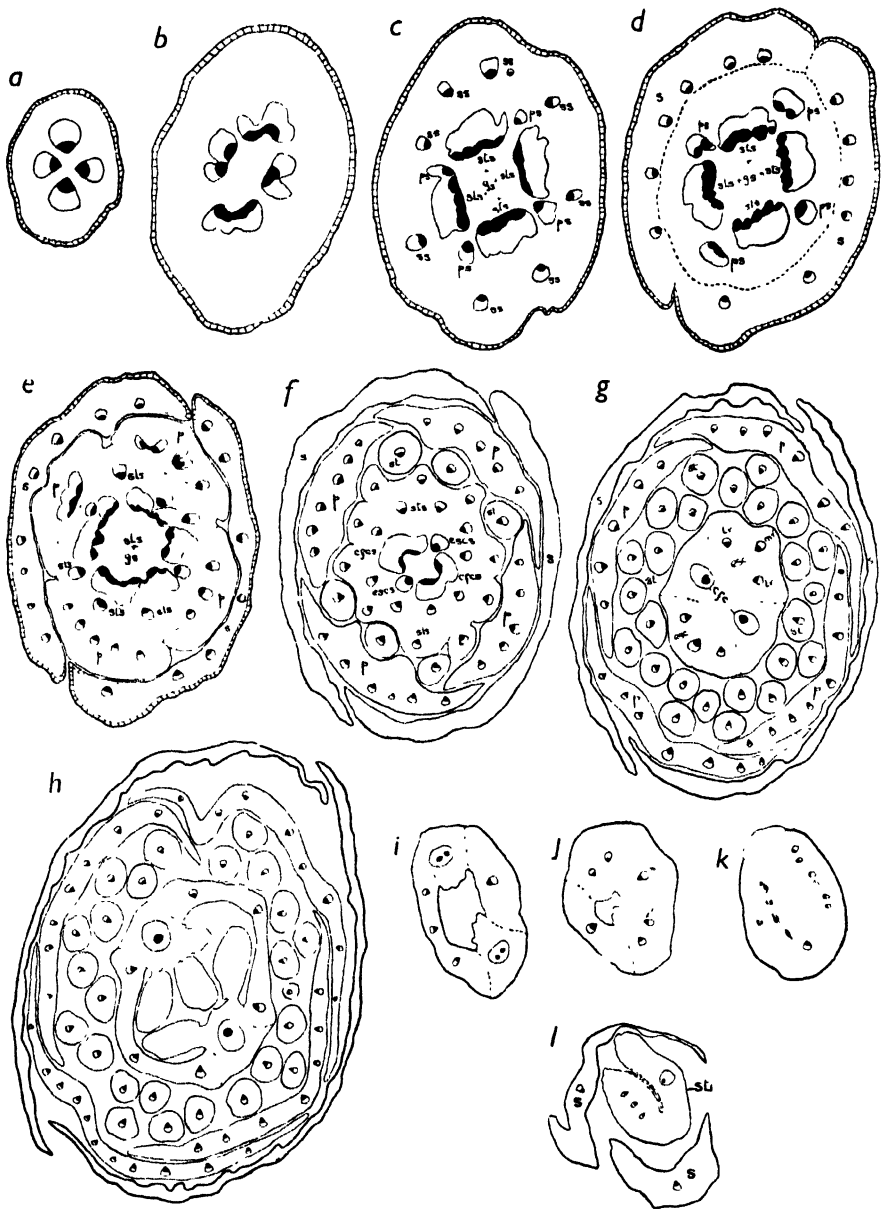


FIG. 18.—*Chelidonium majus* L.

a, b. Primary bundles in floral axis.

c, d. Derivation of sepal-supplies (ss.), petal-supplies (ps.), and vascular groups which ultimately supply androecium and gynaeceum (sts.+gs.).

e. Sepals (s.), petal bases (p.), androecium- and gynaeceum-supplies (sts.+gs.).

f. Sepals and petals *in situ*, stamens (st.) becoming free from the receptacle and amalgamation of gynaeceum-supplies into four groups (escs., cfs.).

g, h. Development of gynaeceum.

i-k. Division of bundle in contracted carpel and formation of style and stigma (sti.).  
( $\times 35$ .)

is perhaps an indication that the marginal strands, when the carpel is full formed, have gradually turned inwards, in a similar manner to those of *Sanguinaria*, but exhibiting a greater degree of contraction (fig. 18, f-h).

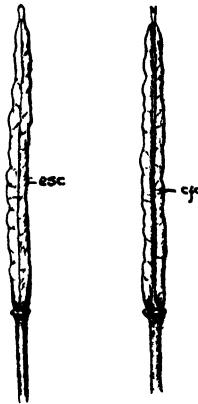


FIG. 19.—Fruits of *Chelidonium majus* L. showing the position of the stigmatic lobes. (Nat. size.)

#### 8. *MACLEAYA CORDATA* (Willd.) R. Br.

In the small peduncle of *Macleaya cordata* (Willd.) R. Br. there are four large vascular bundles. These are comparable with those in the peduncle of *Chelidonium majus* in that they are of triple constitution (fig. 20, a, b). In *Macleaya*, however, the two middle strands of the four allotted to each sepal fuse immediately, so that only three strands actually enter into each sepal base, while in *Chelidonium* the four strands remain distinct at the base of the sepal (fig. 20, b-d).

The species of *Macleaya*, with those of the closely related *Bocconia*, are the only members of the Papaveraceae in which the petals are absent, and so far no traces of vascular supplies apparently destined for the petals have been found.

When the sepal supplies have been formed, there remain in the centre of the axis four uneven groups of vascular tissue. These fuse into an irregular circle from which the vascular supplies of the indefinite staminal whorls arise (fig. 20, c-e).

When the staminal whorls have been completed, lying in an almost even ring so that it is difficult to distinguish between an outer and an inner whorl, there are four remaining vascular strands; as in *Chelidonium*, one pair is larger than the other. These form the carpellary supplies, and in this genus also there are two expanded sterile carpels and two contracted fertile carpels; the two smaller strands supply the expanded and the two larger supply the contracted carpels (fig. 20, e-h). In a gynaecium from a young flower-bud the divisions of the four carpels are hardly distinguishable from each other, but the differentiation is clearly seen when the ovary becomes more mature.

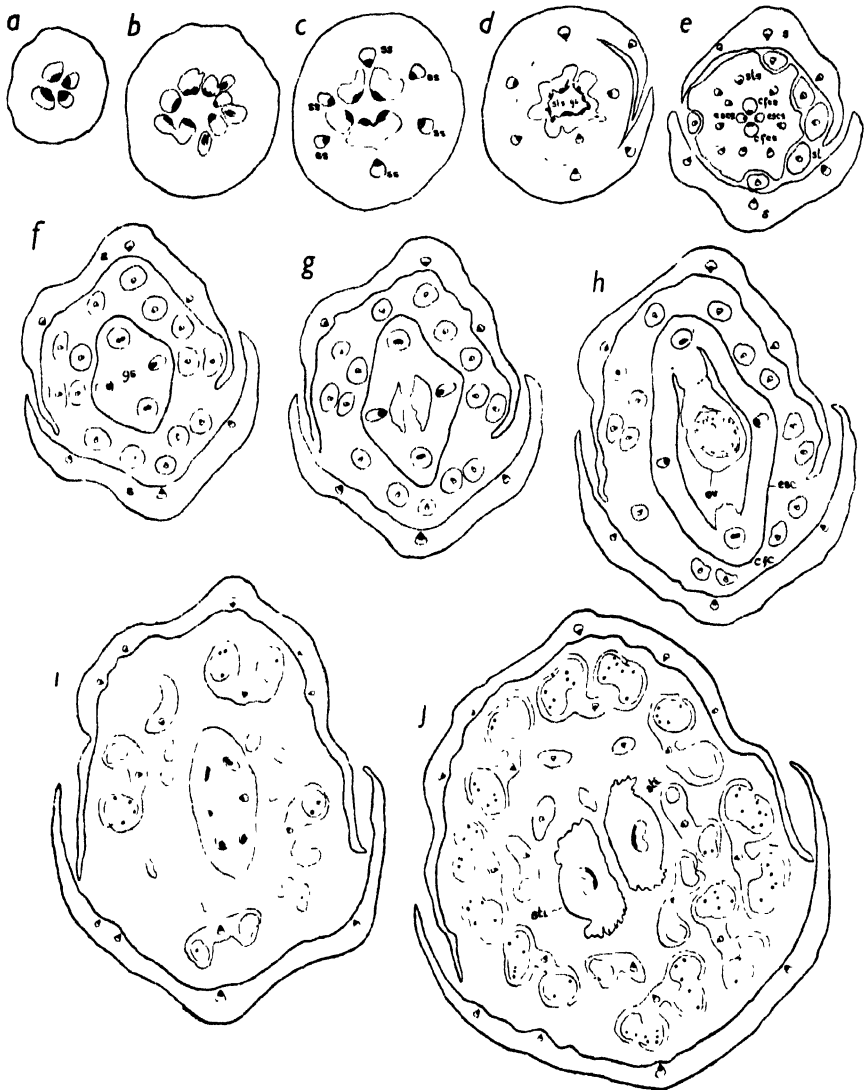


FIG. 20.—*Macleaya cordata* (Willd.) R. Br.

*a-d.* Receptacular bundles and derivation of sepal strands (*ss.*).

*e-h.* Derivation of stamen-supplies; development of gynaeceum (*gs.* and *scs.*, *efcs.*) and production of an ovule.

*i, j.* Division of the bundle in contracted carpel and formation of style and stigma. ( $\times 35$ .)



The large concentrated bundles in the contracted carpels divide into two parts at the top of the gynaecium, which is surmounted by a short style and two small stigmatic lobes. The lobes are situated over the expanded carpels and each receives three small vascular strands; these strands are derived from the midrib of an expanded carpel *plus* half the bundle of each contracted carpel ( $\frac{1}{2} + 1 + \frac{1}{2}$ ), but they show as three strands only in the style, for they unite into an elongated group in the actual stigma-lobes (fig. 20, i, j).

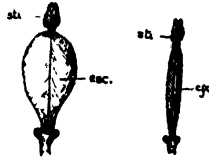


FIG. 21.—Fruits of *Macleaya cordata* (Willd.) R. Br., showing the position of the stigmatic lobes. ( $\times 2\frac{1}{2}$ .)

#### 9. ESCHSCHOLTZIA CAESPITOSA Benth.

The vascular system in the slender peduncle of *Eschscholtzia caespitosa* Benth. consists of several (five in the specimen here described) irregularly shaped bundles of unequal size. As the stem develops towards the flower, the bundles also increase in size and, finally, just below the base of the receptacular cup, they fuse into a ring (fig. 22, a).

From this ring, at a slightly higher level, very small strands separate to supply the 'sepal cap', i.e. the fused sepals; there is no definite indication as to the number of sepals constituting the 'sepal cap' (fig. 22, b *et seq.*).

The central ring is then broken up again into several (typically four) irregular groups. These develop in a somewhat peculiar manner, for portions of each of the four main groups remain in position and ultimately form the petal supplies, while the rest of the portions move in towards the centre of the axis (fig. 22, b, c). The portions which now lie in the centre fuse roughly into a second vascular ring, and from this, at points opposite the petal groups, the vascular supplies of the androecium arise and move out towards the four petal groups with which they ultimately fuse (fig. 22, c-e).

From the vascular ring which now remains in the centre of the axis the strands of the carpels are derived (fig. 22, d-f). The gynaecium, which arises from the base of the hollowed floral axis, exhibits differentiation of carpels. The primary vascular supply to each expanded carpel is three separate bundles, namely, a midrib and two laterals, but when fully developed there are five main strands with several small veins alternating with them. It appears that two extra lateral bundles arise from the vascular masses, from which also the contracted carpel-supplies are ultimately derived, but before they are fully differentiated (fig. 22, e).

The contracted carpels are extremely concentrated and, typically, have only one vascular strand (cf., however, the contracted carpel-supplies in a specimen of *Eschscholtzia californica* (fig. 23), and note the inverted lateral strands in the contracted carpels).

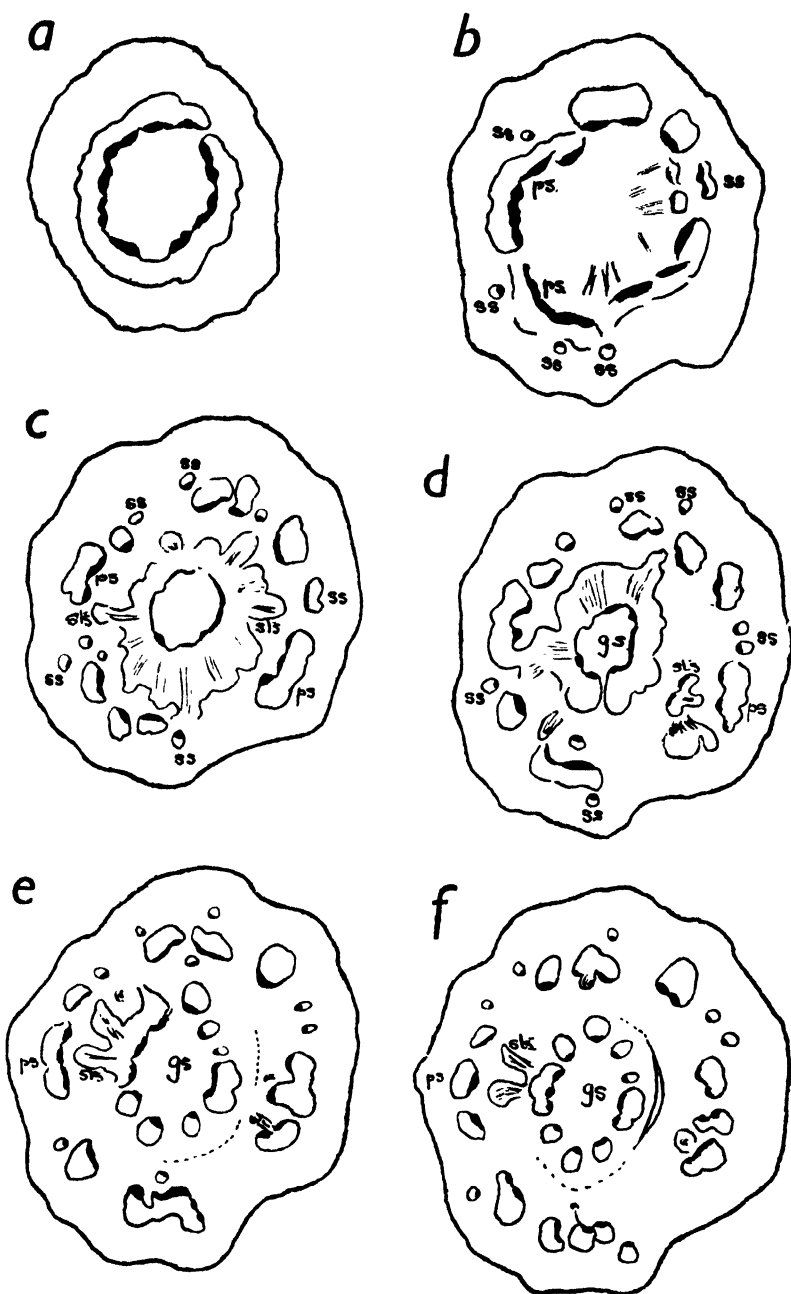


FIG. 22.—*Eschscholtzia caespitosa* Benth.

a. Vascular tissue in pedicel below receptacular cup.

b. Derivation of sepal strands (ss.).

c-f. Sepal strands (ss.), petal strands (ps.), and stamen strands (sts.), which move from the centre and fuse with ps., also aggregation of gynaecium strands (gs.) into definite formation. ( $\times 35$ )

By the time that the vascular supplies to the carpels have been defined, the irregular masses which supply the four petals have assumed their position in the wall of the receptacle, namely, in four groups, each of which breaks up radially into three definite bundles. Thus each of the four petals, which are arranged in two whorls on the rim of the receptacle, has a triple system at the outset (fig. 24, a, b).

These bundles besides supplying the petals also carry with them the stamen strands. In the specimen here described the androecium consisted of sixteen stamens, and these were derived in a definite manner from the triple supplies of the petals.

As the receptacular cup increases in diameter towards the top, each of the three bundles in each of the four petal groups divides in line with the circumference of the receptacle so that the true petal-supplies are once more differentiated from those of the stamens (fig. 24, c, *ps.*).

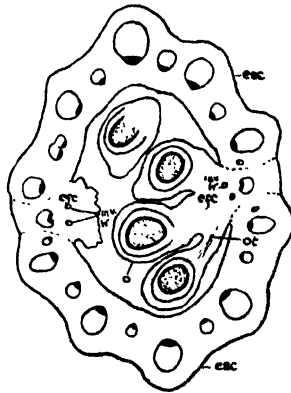


FIG. 23.—*Eschscholtzia californica* Cham.

T. S. of gynaecium showing inverted lateral strands (*inv.lr.*) in concentrated fertile carpels (*cfc.*). ( $\times 35$ .)

As soon as the petal-bundles become free, the staminal strands begin to move into their appropriate positions, and it is now that the definite derivation of the stamens becomes apparent (fig. 24, c; fig. 25, a, b).

It has already been noted that the petals are arranged in two whorls, an inner and an outer. The three staminal bundles which arise from the three strands of each of the inner petals remain intact and each strand provides a single stamen. The strands which arise from the outer petal-traces behave in a somewhat different manner. The central one of the three remains unchanged, but the two lateral strands divide again so that the number of staminal strands which lie opposite the outer petals is five (fig. 25, a, b).

The innermost portions of the now divided strands move slightly towards the 'inner petal stamens', so that when the filaments ultimately become free from the receptacle there is no one directly in front of another.

The derivation of the vascular strands to the four stigmas in *Eschscholtzia caespitosa* is somewhat unusual. As the gynaecium tapers towards the top the subsidiary strands die out, leaving five strands in each expanded carpel

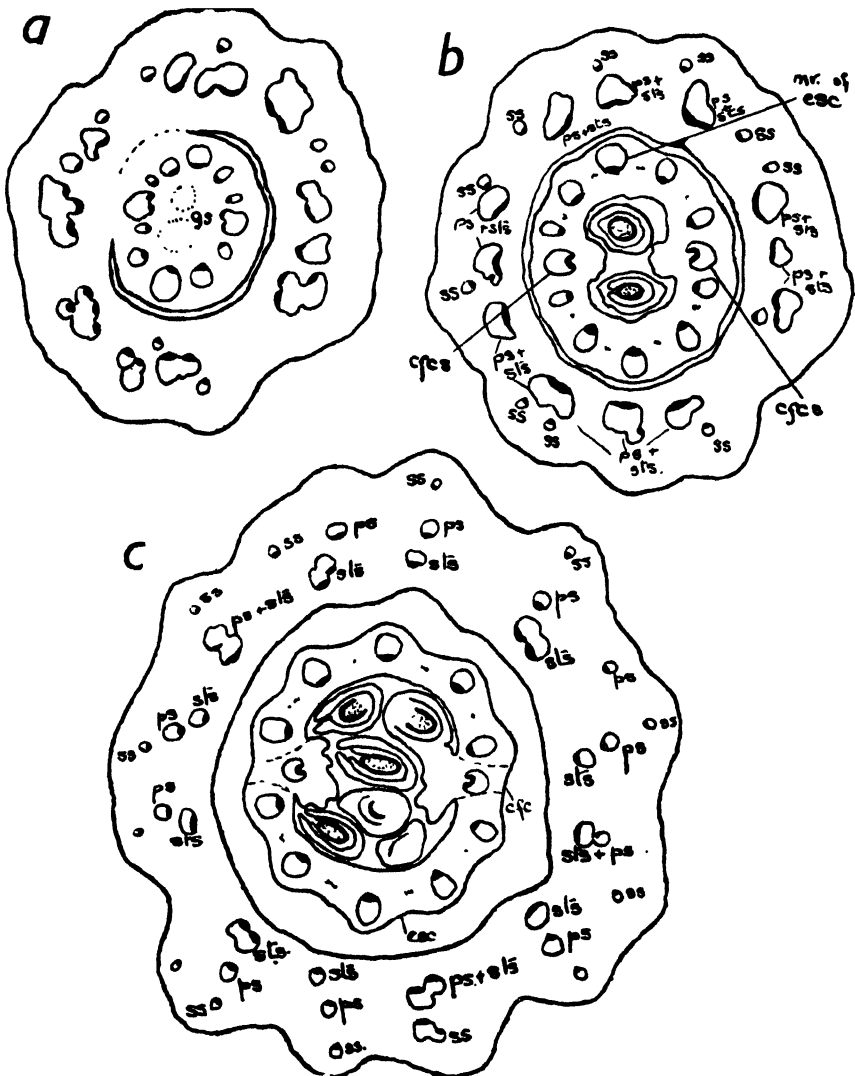


FIG. 24.—*Eschscholtzia caespitosa* Benth.

a-c. Showing gynaecium within hollowed receptacle which contains sepal strands (ss.) and petal fused with stamen strands (ps.+sts.). ( $\times 35$ .)

and one in each contracted carpel, thus the total number is twelve strands. On the formation of the stigmas, the top of the gynaecium divides into four portions, each containing three vascular strands. By this procedure a stigma

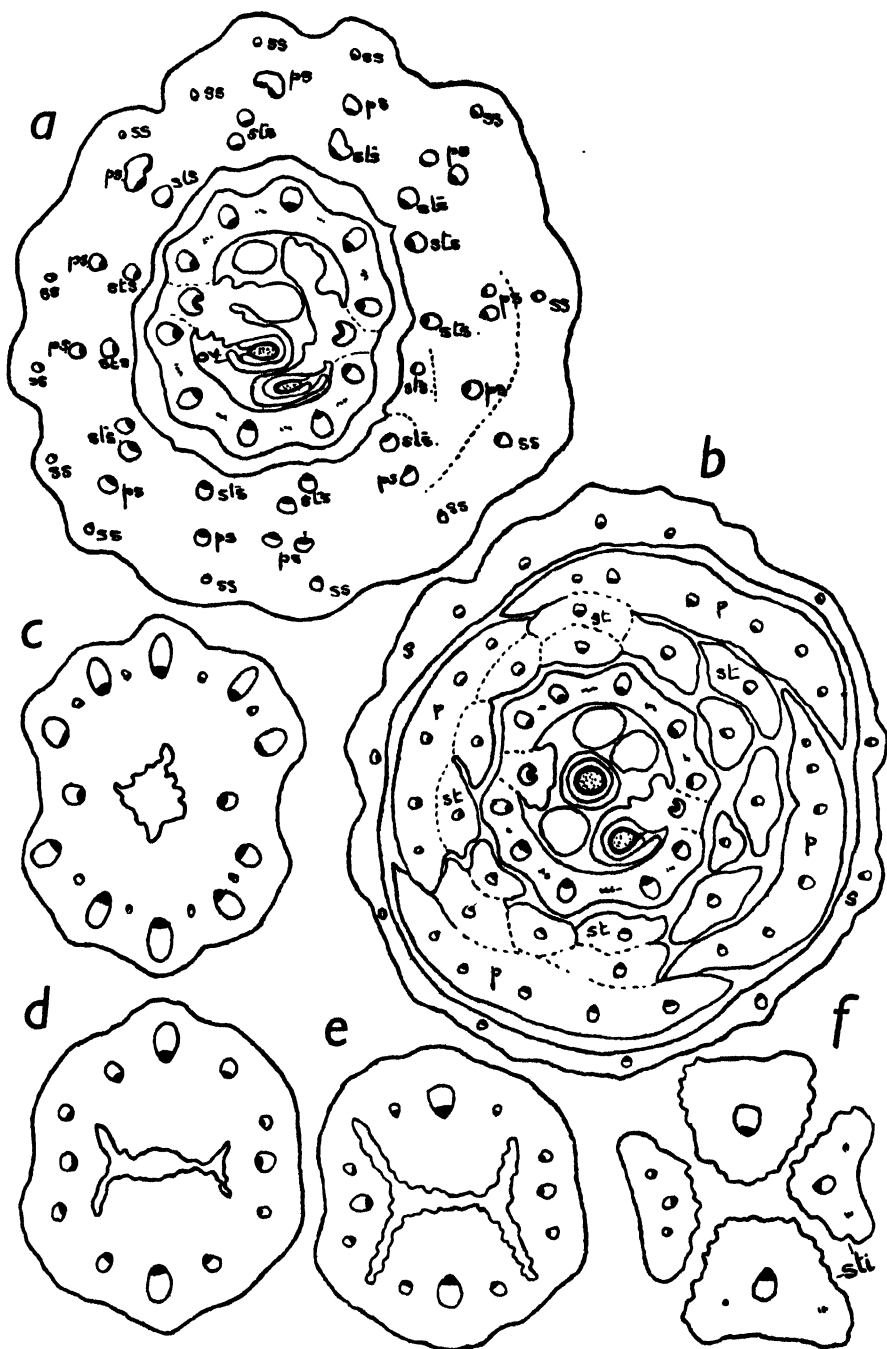


FIG. 25.—*Eschecholtzia caespitosa* Benth.

- a. Fully formed gynaecium with ovules (ov.), petal strands (ps.), separating from stamen strands (sts.).  
 b. Differentiation of sepal-cap, petals, and stamens.  
 c-f. Derivation of stigmas from contracted apex of gynaecium. ( $\times 35$ .)

which is situated over a contracted carpel receives the strand of that carpel *plus* one of the four lateral strands from each of the adjoining expanded carpels (fig. 25, c-f).

The formation of the stigmas in *Eschscholtzia californica* is somewhat different. In this species the five main vascular strands in each of the expanded carpels

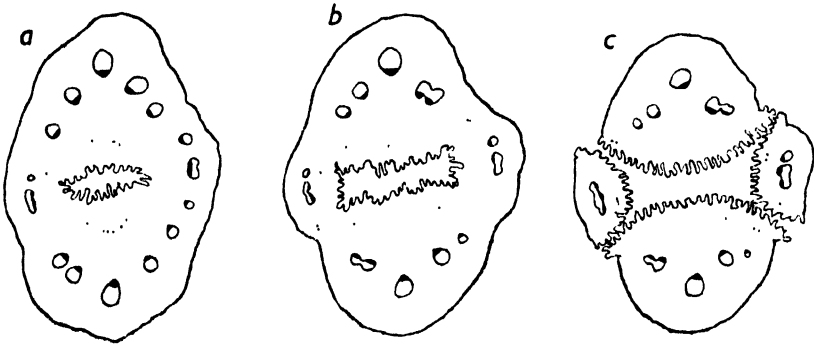


FIG. 26.—*Eschscholtzia californica* Cham.  
a-c. Formation of stigmas (cf. *E. caespitosa*). ( $\times 35$ .)

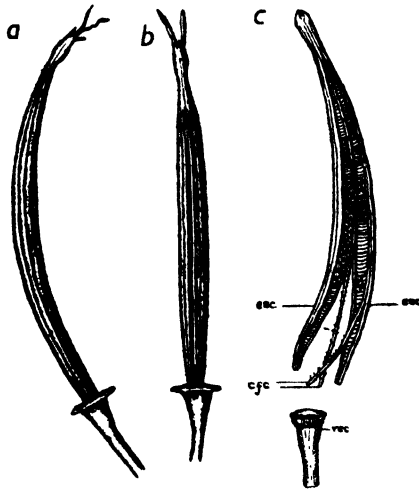


FIG. 27.—*Eschscholtzia californica* Cham.

a, b. Fruits.

c. Fruit showing method of splitting, four carpels becoming free from each other. ( $\frac{1}{2}$  nat. size.)

tend to fuse at the apex of the gynaecium, and the single strand in the contracted carpels tends to break up into three portions. A stigma is developed over each carpel and its vascular supply is derived solely from the strands of that particular carpel (fig. 26, a-c).

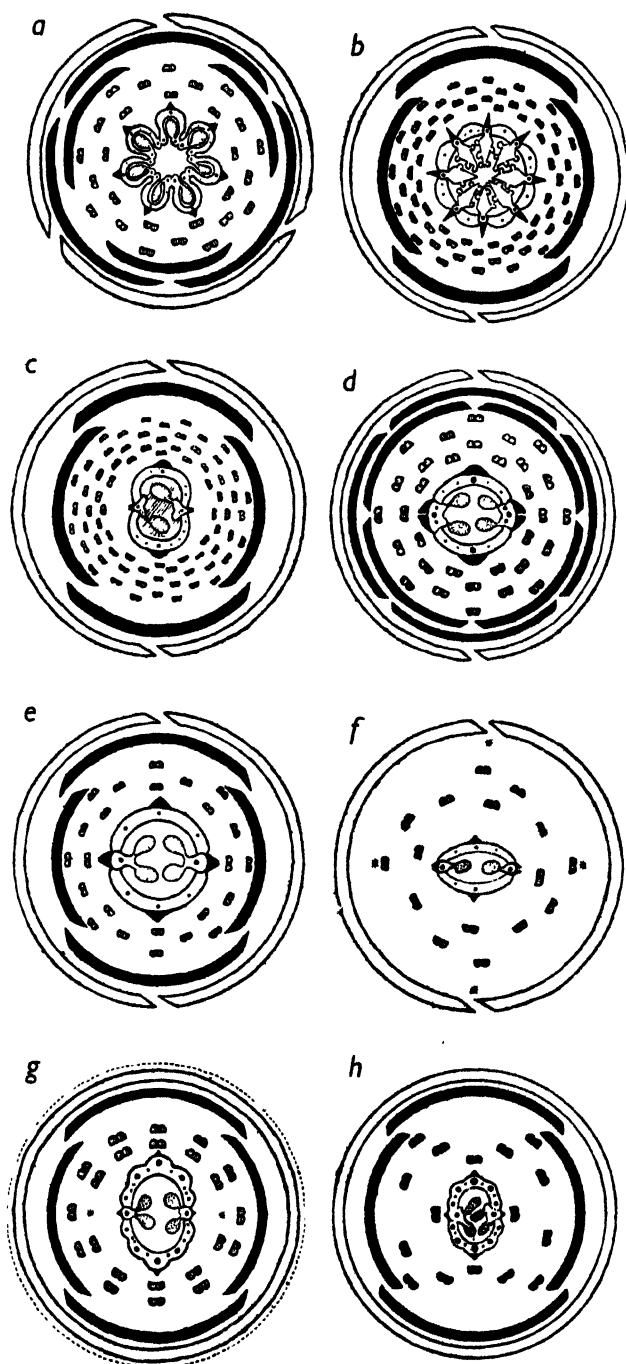


FIG. 28.—Floral diagrams of :—a. *Platystemon californicus*. b. *Papaver Rhoeas*. c. *Glaucium flavum*. d. *Sanguinaria canadensis*. e. *Chelidonium majus*. f. *Macleaya cordata*. g. *Eschscholtzia californica*. h. *Eschscholtzia caespitosa*.

As it ripens, the ovary of *Eschscholtzia* spp. gradually becomes curved with a contracted carpel on the inner and the outer edge of the curve (fig. 27, a, b). When dehiscence occurs, the fruit splits down the lines of fusion between one of the expanded carpels and the contracted carpel on the outer edge. The split edges then bend inwards in such a way that the expanded carpels form two boat-shaped cavities in which the seeds are protected while still fixed to the contracted carpels (fig 27, c). When the two expanded carpels do eventually separate from each other, each of them usually has one contracted carpel adhering to it, and it is only when the fruit is withering, after the seeds have been dispersed, that the four carpels become entirely free from one another.

The ovary, at maturity, is fixed very lightly to the base of the receptacular cup and easily becomes detached if the slightest strain be put upon it. If it is pulled out of the cup, it generally splits at once up both sides with some force, and, not infrequently, the expanded carpels break away from the contracted members, thus showing that the ovary is distinctly made up of four parts.

Lindley (19) claimed that there are multiple rows of ovules in *Eschscholtzia*, but the idea was probably founded on the fact that a transverse section of the gynaecium shows numerous ovules apparently arranged in rows. Actually the ovules are so closely packed in the ovary that the funicles of two or more may be almost side by side, and a section taken at any point will therefore cut through several ovules, though they are not exactly at the same level. An examination of a mature contracted carpel, from which the seeds have fallen, will clearly demonstrate this point.

## II. COMPARISON OF TYPES.

A cursory examination of the floral characters of various members of the Papaveroideae may lead one to assume that there are certain main types, or groups, in this subfamily, and that the members of a group resemble one another very closely.

*Glaucium* may be associated with *Sanguinaria*, *Chelidonium*, *Macleaya*, and *Eschscholtzia* on account of these genera exhibiting differentiation of carpels (though the actual shape of the gynaecium is variable).

At the extreme base of the ovary in *Glaucium flavum* there are four groups of vascular tissue, one for each carpel. As soon as the carpel begins to develop, the groups break up into definite vascular strands, but the number and position of these strands, with the exception of the midribs of the expanded carpels, are not fixed at any level in any individual; in this respect *Sanguinaria* resembles *Glaucium*.

*Chelidonium* and *Macleaya* also have four primary vascular supplies to the gynaecium, but both of these plants have only one concentrated strand in the contracted carpels, and, in most cases, there is a definite number of strands in the expanded carpels, namely, a midrib and two laterals.

The primary strands to the ovary in *Eschscholtzia* differ from those of *Glaucium*, *Sanguinaria*, *Chelidonium*, and *Macleaya*. In this genus there are eight groups



of vascular tissue, one to each contracted carpel and three to each expanded carpel. The two lateral strands in the expanded members typically divide again, so that, when the carpels are fully formed, there are five main strands in each.

Like that of *Sanguinaria*, a semi-mature ovary of *Glaucium* has numerous strands in all four carpels, whereas *Eschscholtzia* has definitely five main bundles in each expanded carpel with one to three subsidiary strands between the ribs ; the contracted carpels of *Eschscholtzia* contain one mass of vascular tissue which tends to take a crescent-shaped formation.

The vascular supplies to the ovary in *Chelidonium* and *Macleaya* are somewhat similar ; in each there is one concentrated bundle in the contracted carpels and three principal strands in the expanded carpels.

*Glaucium flavum* has a peculiarity in the gynaecium which is not found in any other genus in the Papaveroideae, namely, the ' false septum ' that is developed after fertilization.

There is considerable variation in shape and formation of the stigmas in the Papaveroideae. The capsular fruits in *Papaver* are surmounted by a flat, or sometimes conical, cap with as many rays of velvety stigmatic papillae as there are placentae. In *Papaver* the rays are situated over the placentae and are provided with vascular strands from the contracted carpels only.

*Glaucium flavum* has a large compound stigma consisting of two roughly triangular lobes which are situated over the expanded carpels. The vascular system of each lobe is made up of the strands of an expanded carpel *plus* half the strands of each contracted carpel. The stigma in *Macleaya* appears as two small blunt lobes, and it is derived in the same way as that of *Glaucium* and *Chelidonium*. In *Platystemon* and *Eschscholtzia* each carpel ends in a long slender stigma. Each individual stigma is provided with three weak vascular strands, which are derived from the strands of the carpel which it surmounts. (A slight variation in the origin of the vascular strands to the stigmas in *Eschscholtzia caespitosa* has already been noted.)

The way in which the capsules of the various genera eventually split provides another point of comparison. In *Glaucium* the expanded carpels split off from the top downwards and this also occurs in *Macleaya* ; in *Papaver* the capsule opens at the top, but here dehiscence is by pores situated at the tips of the expanded carpels and formed by the lifting of the persistent stigmatic cap, by the elongation of the placental ribs. In *Chelidonium* the expanded carpels separate from the bottom upwards, and ultimately this also occurs in *Eschscholtzia*, but as the base of the ovary is constricted and held by the cup-shaped receptacle, the expanded carpels do not come apart so readily.

Although the stamens in the Papaveroideae are very indefinite and fluctuate in number, the primary supplies are typically in four groups. The formation of the staminal whorls of *Glaucium* is very similar to that of *Papaver* ; the stamens separate from the central column practically one behind the other, but gradually assume a somewhat irregular spiral pattern,

The stamens of *Chelidonium* and *Eschscholtzia* somewhat resemble each other in numbers, but not in vascular origin and final arrangement. In *Chelidonium* there are definitely three whorls originating in the four primary vascular groups and each consisting of about eight stamens which alternate with one another.

The origin of the stamens in *Eschscholtzia* is very different. *Eschscholtzia* is a perigynous flower, and therefore the sepal, petal, and stamen supplies are more or less fused to each other in the wall of the hollow receptacle. The sepal strands split off quite near the base of the cup, but the petal and stamen strands remain fused for some distance. Eventually the petal-supplies separate and leave typically twelve bundles from which the stamens arise.

The stamens in *Macleaya* appear to have no definite plan, except that they arise from the four groups of vascular tissue in the centre of the axis.

With regard to the petals, there are two main types of flower in the Papaveroideae, namely, those with six petals as in *Platystemon*, *Platystigma*, and *Romneya*, and those with four as in *Glaucium*, *Papaver*, *Chelidonium*, *Eschscholtzia*, &c., but in several members of the subfamily the number is not fixed. *Argemone* has from four to six and *Sanguinaria* from eight to twelve (typically eight) petals. *Macleaya* and *Bocconia* stand apart from the other members in having no petals.

There is, however, a considerable variation in the formation of the petals of different members of the same type. In *Platystemon* one strand is allotted to each petal, but this divides into three before it enters the base of the limb. In the second group three is the common number of primary vascular strands to each petal; *Glaucium* and *Eschscholtzia* have three strands, *Papaver* has three to numerous, but *Chelidonium* usually has only one, which divides into three as soon as it enters the base of the petal.

There are two main sepal types in the Papaveroideae, namely, flowers with three sepals (six petals) as in *Platystemon* etc. and flowers with two sepals (four petals) as in *Glaucium* etc. *Argemone* appears to be in a transition-stage between parts in threes and parts in twos, as the petals vary from four to six and the sepals from two to three.

In *Papaver Rhoeas* the development of the vascular strands in the axis which supply the sepals is almost the same as in *Glaucium flavum*, but in *Chelidonium* and *Macleaya* the supplies are derived in a somewhat different manner, for though they arise from the axial bundles in a similar way the strands do not break up in the receptacle as they do in *Glaucium* and *Papaver*, but typically remain entire until they have entered the bases of the sepals. *Macleaya* exhibits a slight difference from *Chelidonium*, for while both plants have four strands allotted to each sepal, those in *Chelidonium* remain as four until they branch within the sepal, but in *Macleaya* the two innermost ribs of the sepal fuse in the axis before the limb is reached, so that actually there are only three ribs in each sepal.

### III. PREVIOUS INTERPRETATIONS AND DISCUSSION.

Saunders \* asserts that the stigmas in *Glaucium flavum* are situated over the placentae, i.e. over the fertile carpels—an opinion also held by Hooker (13); it appears, however, that the statement needs some amplification and explanation.

Serial sections through gynaecia of *Glaucium flavum* in varying stages of development show that the apex of each triangular stigmatic lobe is centred over the expanded sterile carpel and not over the contracted fertile carpel. The actual vascular anatomy shows, as Saunders notes, the strands of  $\frac{1}{2} + 1 + \frac{1}{2}$  carpels, but in the reverse order, namely, half fertile *plus* sterile *plus* half fertile, instead of half sterile *plus* fertile *plus* half sterile. The same vascular construction of the stigmas occurs in *Macleaya*, *Sanguinaria*, and *Chelidonium*.

Eames (5), however, does not agree with the theory of  $\frac{1}{2} + 1 + \frac{1}{2}$  development of the vascular supplies to the stigmas, whether they are commissural or non-commissural.

It has been concluded, up to the present, by prominent morphologists that the commissural stigma has been formed from 'the united halves of stigmas normally placed which have migrated laterally and fused' (cf. 5, p. 184). In such forms the placental, i.e. marginal, vascular strands may, or may not, enter the stigma. In those plants with bi-carpellary ovaries in which these strands *do* run up into the tissues of the stigma, the organ must, *ipso facto*, be composed of half the strands of two distinct carpels.

If this is so, there seems to be no reason why the dorsal rib of a contracted carpel cannot divide in a like manner and the two halves unite either with the stigma surmounting the expanded carpel or the behaviour may be as in *Papaver*, where the stigmas formed from the placental strands, i.e. the fertile carpels, fuse by their margins over the sterile carpels, for in this plant the tips of the expanded carpels are never actually united with the stigmatic cap; therefore the strands of the expanded carpels do not constitute any part of the vascular supply to the stigma. Where the expanded carpels are fused with the stigmatic region there is no reason why their strands should not continue in a straight course and run up into the stigma. Or—and this seems to be a likely suggestion—the expanded carpel provides a stigma as well as the contracted carpel, and the branches of the 'placental' stigma, when it divides into two parts, fuse with the neighbouring stigma which surmounts the expanded carpel. (These last two points are illustrated by the development of the stigmatic lobes in *Glaucium flavum*.)

\* Saunders (24, p. 51) makes the statement that 'The stigmas in all the Papaveroideae (*Romneya Coulteri* Harv. included) are commissural, except in *Platystemon* and *Platystigma*, where they are centred over the sterile carpels (in other words, are alternate with the placentae) and in some flowers of *Eschscholtzia* (previously described), where they are developed on the valve as well as on the solid carpels'.

I have assumed that the above statement covers all the plants of the subfamily that are mentioned in this communication, but, as Saunders gives no definite description of many of the types, the comparisons made here can, to some extent, be only tentative,

It is well understood that a fairly constant system of division of labour is to be found among the parts of a plant ; therefore when carpels have become so modified that their work is concentrated solely on the production of ovules, it is not unlikely that these organs, so highly specialized in one direction, will not have such strongly developed stigmas as have the expanded sterile carpels. This point is well demonstrated in *Eschscholtzia californica*.

Specimens of this plant were found with stigmas of varying size and number ; in some there were four well-developed stigmas, one arising from each of the four carpels, but more frequently there were two fully developed organs surmounting the two sterile carpels and two lesser ones on the fertile members, while it was not uncommon to find specimens with only the two sterile carpel stigmas and the other two reduced to mere points on the tips of the fertile carpels.

Eames (5), while repudiating the theory that the vascular strands of a stigma may be derived from two different carpels and from carpels which are not in the same whorl (p. 185), yet says that 'vascular bundles which lie close to one another become fused whenever the union of the carpels has become intimate' (p. 166). He even goes so far as to say that 'fusion occurs as readily between vascular bundles of organs of different whorls as between those of the same whorl', for 'whenever bundles lie close to one another radially or tangentially they may become fused' (p. 169).

The ventral strands of a carpel often die out, therefore a non-commissural stigmatic lobe on a gynaeceum exhibiting differentiation of carpels may quite well have three strands consisting of the dorsal strand of the expanded carpel *plus* half the dorsal of each contracted carpel ; this appears to be so in *Sanguinaria*.

All the types of the Papaveraceae here investigated that showed differentiation of carpels, with the exception of *Papaver*, *Argemone*, and *Meconopsis*, have 'non-commissural' stigmas ; *Eschscholtzia*, of course, stands apart in having both 'commissural' and 'non-commissural' stigmas.

But the question arises whether there is such a thing as a 'commissural' stigma in the Papaveroideae ? The answer is that, as a true commissural stigma is one that is situated over the fused margins of a normal carpel or carpels, definitely there is not, for the alleged commissures are not fused fertile margins, but a distinct whorl of contracted fertile carpels which are surmounted by the stigmas.

There seem to be varied opinions as to the position of the stigmatic lobes in *Chelidonium majus*. Kirk (16) and Hooker (13) say that they are opposite the placentae, while Carter (4) says that they alternate with the placentae. The latter interpretation appears to be correct, for though the lobes frequently appear to be over the placentae, if their development is traced through serial sections, it is easily seen that this appearance is due to a twist in the style which takes place as the ovary matures, and has no connexion with the formation of the stigmatic lobes,

It should be noted that the fruits of the Papaveroideae may be placed in, roughly, three groups: firstly those which are composed of numerous normal carpels, either free (ultimately) or fused, i.e., *Platystemon*, *Platystigma*, and *Romneya*; secondly, those which show differentiation of the numerous carpels and have ovoid capsular fruits, i.e. *Argemone*, *Papaver*, and *Meconopsis*; and, lastly, those which show differentiation, but are reduced to siliqua-like structures composed of four carpels, i.e. *Glaucium*, *Sanguinaria*, *Chelidonium*, *Macleaya*, *Eschscholtzia*, &c.

Of all the members of the Papaveraceae that have been examined the gynaeceum of *Platystemon* seems to present the fewest difficulties with regard to structure and development. It is composed of numerous normally-formed multi-ovulate carpels, which are, however, in an immature gynaeceum, fused very lightly with one another. The stigmas are developed over and from the midribs of the carpels, and the ventral, or placental, strands become very weak and may, or may not, enter the stigma.

Rendle (21), Warming (26), and Kirk (16) all agree that the gynaeceum in *Platystemon* is made up of numerous free, or partially free, carpels; Rendle also notes that 'the style is a continuation of the middle line of the carpel and bears the stigma', while Warming points out that the carpels are 'transversely divided and constricted into joints which separate as nut-like portions'. Kirk's description as far as it goes is perhaps the most accurate, for he says that the pistil is composed of several ovaries which are joined together at first, but which separate from one another, when ripe, into narrow pods.

Saunders (24) interprets the gynaeceum of *Platystemon* in an entirely different manner. She says that the midrib of that which, in this paper, is termed a normal carpel represents a 'solid sterile carpel'; and that the two fertile margins of the carpel (the vascular supplies of which are derived from the ventral strands in the usual manner) are semi-solid fertile members. The stigmas are, she says, 'centred over the sterile carpels' and have the  $\frac{1}{2} + 1 + \frac{1}{2}$  vascular system, but here again her interpretation has gone astray, as there appears to be absolutely no indication of any such formation.

The gynaeceum of *Platystemon* is of such straightforward and simple construction that there seems to be no need for the complicated interpretation given by Saunders, and after the examination of serial sections there appear to be no foundations (in this case, at any rate) on which to build the 'polymorphism' theory, for the carpels are derived in a very similar manner to the follicles figured and described by Eames and Wilson (7) as typical examples.

There is one slight difference between the follicular carpels figured by Eames and Wilson and those of *Platystemon*—that is, their position on the receptacle. *Platystemon* has an almost flat receptacle and therefore the carpels are arranged in a ring, whereas the typical follicular types frequently have a somewhat conical receptacle, in which case the carpels are arranged in spirals up the cone.

This point, however, does not interfere with the actual vascular anatomy of the carpels.

*Platystemon* belongs to what may be regarded as the most primitive group of the Rhoeadales, and appears to provide a definite link with the Ranales through the formation of the gynaeceum.

*Platystigma* also belongs to the *Platystemon* group, but in this plant the gynaeceum is composed of three (rarely four) fertile expanded carpels fused by their margins, which produce ovule-bearing placentae. As in *Platystemon*, the stigmas are developed from the midribs. Saunders, in accordance with the 'polymorphism' theory, says that in *Platystigma linare* there are six carpels, namely, 'three solid, or very contracted, sterile valve carpels alternating with three fertile, semi-solid carpels (G 3+3)', and that the stigmas have  $\frac{1}{2}+1+\frac{1}{2}$  formation and alternate with the placentae.

Unfortunately the only species of this genus that was obtainable was *Platystigma oreganum* Benth. & Hook. fil., so that a comparison of descriptions could not be made, but there is evidence that it is quite unnecessary to give the structure of the gynaeceum in *Platystigma oreganum* such a complicated interpretation.

*Romneya*, the last of the three types in the first group, has numerous normal carpels which are fused into a multi-locular ovary that is surmounted by a cluster of somewhat short fleshy stigmas. Hooker (12) and Baillon (2) are both of the opinion that the stigmas in this plant are non-commissural, but Harvey (11) states that they are opposite the placentae. Saunders is in agreement with the latter theory, and she also claims that the stigmas have the  $\frac{1}{2}+1+\frac{1}{2}$  vascular system.

The anatomy of the gynaecea of the *Papaver* types, i.e. *Papaver*, *Argemone*, and *Meconopsis*, appears to have escaped any very detailed examination. Saunders, however, found that there were two kinds of carpels in the capsule of *Papaver*, and I can confirm that the gynaeceum in this genus exhibits differentiation of carpels.

It has been shown that the gynaeceum in *Glaucium flavum* is made up of an outer whorl of two expanded sterile carpels which practically inclose an inner whorl of two contracted fertile members. This form of ovary is found throughout the Cruciferae and frequently in other members of the Rhoeadales. Over a hundred years ago, Lindley (19) came to the conclusion that the definition of a Cruciferous fruit should be as follows:— 'Pericarpium formed of four confluent pistilla, of which two are placentiferous and furnished with stigmata and two destitute of placentae and stigmata, but separable in the form of valves', and this definition is applicable, excluding the reference to the stigmas, to all the siliqua-shaped gynaecea in the Papaveroideae.

This discovery has been confirmed by Eames and Wilson as well as by Saunders (22), but while the former point out that this type of gynaeceum is due, at least in the Cruciferae, to 'an extreme modification of a normal carpel', the latter claims that there are present in the Crucifers 'carpels of different structural types, fulfilling different functions'.

Arber (1), on the other hand, continues to uphold the theory of the bi-carpellary construction of the Cruciferous gynaeceum. She concludes that the

'replum bundles' of a Cruciferous ovary do not represent those of a distinct whorl of carpels, but are simply the fused ventral strands of two normal carpels, and though she makes especial note of the inverted strands she does not rightly interpret their derivation.

In her description of the development of the inverted bundles, Arber indicates that they are derived from both the 'valve bundles' and the 'replum bundles'. This does not seem to be a quite accurate interpretation, for the vascular strands which remain in the axis immediately after the separation of the stamens from the receptacle must not be regarded as definitely allotted strands to definite carpels. They must be regarded as a residual group of vascular strands from which, ultimately, after a certain amount of re-arrangement, the carpel-supplies are derived.

In the Cruciferous types the first strands to become definitely differentiated are the dorsal ribs of the expanded sterile carpels. The strands of the contracted carpels now begin to take up their position, but owing to the contraction of the carpels they are frequently irregular in shape on account of their composite nature, for the subsidiary laterals of the contracted carpels are usually fused with the midrib. The small bundles which lie between these four main vascular masses are still of the residual character, and it is from certain of these that the inverted strands, i.e. the ventral strands, of the contracted carpels are derived. The ventral strands of the expanded carpels are derived in precisely the same way, although, of course, they exhibit no inversion of the ventral strands, as the carpels are not contracted.

Arber notes that 'the ovules receive their vascular supply from this inverted bundle', but she gives no explanation as to the reason for this unusual procedure. It seems to be an unnecessary complication if the ovary consists of normal expanded fertile carpels, for the inverted bundles are very much weaker than the strand which, according to Arber's interpretation, is a normal ventral bundle. One would expect the ovule supplies to arise from this strand and not from the inverted one; also the position of the large bundle is much more convenient for ovule-production than that of the inverted strands.

The explanation of this unusual manner in which the ovule-strands are produced is to be found in the four-carpellary interpretation of the Cruciferous gynaecium, according to which these inverted vascular bundles are the normal ovule-producing strands of carpels which have become contracted by the in-folding of the carpel margins, so that the ventral strands have become turned from their usual position, with the xylem facing the centre of the axis, to lie immediately opposite the dorsal strand, with the xylem elements inverted.

I am in agreement with Eames and Wilson (6, 7) regarding the derivation of the Crucifer type of gynaecium, and this type, with slight individual variations, is present in many members of the Papaveraceae. The carpels are distinctly in two whorls and many show the vascular supply similar to that of a normal organ in those which have become modified.

Lindley, in 1828, found that the ovary of *Eschscholtzia* was 'formed of four simple pistilla', and compared it with that of the Crucifers (fig. 29), but he

did not rightly interpret their composition and function. His description is a somewhat confused interpretation of right and wrong, for he says that 'upon opening the pistillum we find that there are two parietal placentae corresponding with the smaller stigmata; and that there are no placentae opposite the larger stigmata; in other words, that it is formed of four simple pistilla, two of which are opposite and ovuliferous, with their placentae in the usual place, alternating with themselves; and two nearly abortive, destitute of placentae, consequently not ovuliferous, and so nearly suppressed by the superior energy of their neighbours that their existence would have been un-

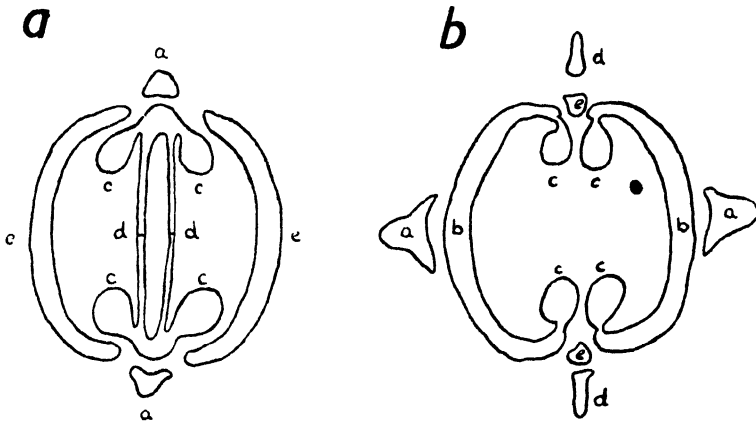


FIG. 29.—*a*. Diagram of a Cruciferous ovary. *b*. Diagram of ovary of *Eschscholtzia*. (After Lindley.)

known but for the stigmata, which indicate their presence. This is one way of understanding *Eschscholtzia*; but as the ovula are not inserted in the placentae in a double row, but rather confusedly arranged in several rows, it may also be assumed that the lateral, imperfect, half-obliterated stigmata have a line of placenta, with ovula appertaining to themselves, but so confused with the placentae of their lateral and more powerful neighbours that, in consequence of their close approximation, they cannot be distinguished.'

Having proceeded so far in his interpretation of the ovary in *Eschscholtzia*, it seems unfortunate that Lindley prefers to adhere to the former of his two opinions, namely, that the expanded carpels bear ovules on their margins and that the contracted ribs are sterile, for the latter is apparently the more correct, though he suggests that both expanded and contracted carpels bear ovules.

Saunders (22) believes that each rib and each intervening furrow in the ovary-wall of *Eschscholtzia* represents a carpel, thus giving a total number of twenty (10, 10). If, however, the development of the gynaeceum is studied from the extreme base and in all stages of growth by means of complete serial sections, it will be seen that this theory cannot be correct.



The primary number of vascular strands at the base of the receptacular cup is typically eight, three for each sterile expanded carpel and one for each contracted carpel. The strand in the contracted carpel remains more or less unchanged and does not divide; but, though the three strands allotted to the sterile carpel may undergo changes and divisions, there is absolutely no evidence which proves that the 'valves' in *Eschscholtzia* are composed of ten 'solid and semi-solid' carpels.

Saunders notes that Lindley 'visualized the fertile carpel contracted to a placentiferous cord, but he failed to perceive the consolidation which produces the multi-carpellary valve . . .'; it was, however, Lindley who was the more correct in the interpretation because he *did* 'fail to perceive' the 'multi-carpellary valve'—a purely imaginary structure, as a systematic study of the gynaecium will show.

Of all the members of the Papaveroideae that have been examined *Eschscholtzia* seems to have reached the highest stage of development; the perianth segments are fixed in number, the stamens are fewer and of much more constant arrangement, the carpels are fixed at four (their supplies are almost definite in number), and the flowers are perigynous, which, according to the generally accepted view, as developed by Wernham (27), is the transitional stage between the primitive types of flowers, such as *Ranunculus* spp. which exhibit hypogyny and the advanced types such as *Pyrus* spp.

In several specimens of *Eschscholtzia californica* very weakly developed, and sometimes abortive, stamens were found, and in both *Eschscholtzia californica* and *E. caespitosa* pairs of stamens will arise from single origins in the axis. These peculiarities in the staminal whorls are perhaps definite indications that in this genus reduction in the number of floral organs is still in progress.

The carpellary vascular strands are much more definite than in the other genera, for, although the weak intermediary strands vary a little, the main strands always remain constant; the fertile members are extremely concentrated so that they appear as the smallest of the ribs on the corrugated ovary.

*Platystemon*, on the other hand, is perhaps the most primitive type in the Papaveraceae, for it is this plant which shows the greatest resemblance to the Ranalean types. Without taking the perianth segments into consideration, though they do show similarity, the androecium and gynaecium have more in common with the Ranunculaceae than with the Papaveraceae. The derivation of the vascular supplies to the carpels in *Platystemon* is practically identical with that of the carpels in *Aquilegia* (Ranunculaceae). It may perhaps be suggested that *Platystemon* forms a direct link with the Ranunculaceae and therefore a connexion between the Ranales and the Rhoeadales.

On examining floral anatomy in detail, one finds that it is extremely difficult to discover any really definite plan or formulate any system of classification of types in any one family, more especially in a family which presents such diverse types as the Papaveraceae.

It is assumed that the family as a whole is comparatively primitive, for there are points of floral structure which apparently link the Papaveraceae with

the Ranalean types which are generally conceded to be basal among the flowering plants.

Difficulties arise when one endeavours to separate the numerous genera of the Papaveraceae into distinguishing classes according to their apparent primitiveness or relationship to the foregoing families, for while a plant may be comparatively advanced in one direction there may be considerable 'lagging' in another.

*Sanguinaria* presents an instance of reduction in the number of carpels and in this respect is qualified to be placed on a level with *Eschscholtzia*, which appears to present the most highly evolved type among the Papaveroideae, but other parts of the flower in *Sanguinaria* still show a plastic arrangement, for this genus is one of the few of the Papaveraceae which have numerous petals.

With regard to the gynaeceum, *Argemone* shows a greater resemblance to *Meconopsis* than to *Papaver*, for *Meconopsis* is a type exhibiting a greater reduction of parts; but then again there is often a tendency for the perianth segments in *Argemone* to be arranged in whorls of three as they are in the more primitive type *Platystemon*.

*Argemone*, *Papaver*, and *Meconopsis* show a much greater degree of consolidation of the fertile carpels than many other members of the Papaveroideae, but in these genera there are numerous expanded and contracted members, whereas *Glaucium* and *Sanguinaria* show a lesser degree of compression, but the actual number of the carpels is reduced to four.

In the first group of the Papaveroideae, i.e. the *Platystemon* group, *Platystemon* is the most primitive type with regard to anatomy, while the other members of the group, *Platystigma* and *Romneya*, appear to provide definite steps towards the second group. Although *Romneya* has an indefinite number of carpels while *Platystigma* has typically only three, the lateral bundles of adjoining carpels are fused in *Romneya*, thus exhibiting a greater state of fusion in the gynaeceum as a whole; the carpels in *Platystigma* are reduced in number, but the lateral strands in adjoining carpels are not fused. It is therefore suggested that *Romneya* is more highly evolved than *Platystigma*.

In the second group, the *Papaver* group, in which differentiation of carpels first makes its appearance in the Papaveraceae, the uneven rate of development of the floral organs makes the arranging of types a little difficult, but on taking all the characters into consideration, the most natural arrangement appears to be:—i. *Argemone*. ii. *Papaver*. iii. *Meconopsis*.

*Argemone* is placed first in the group for several reasons. Perhaps the foremost of these is that the flowers of this genus frequently have three sepals and six petals, and, as this is a definite character of the preceding group, it may be indicative that *Argemone* is, with regard to sepals and petals, in a transition-stage between the two groups.

The main problem that has to be overcome lies in the shape and structure of the style and stigmas, for, while *Argemone* has a cluster of stigmas on a very short style, *Papaver* has no style and *Meconopsis* is characterized by the length of the style.

Although I have not made an extensive examination of *Argemone* and *Meconopsis*, the vascular anatomy of the stigmas appears to be very similar in all three genera and the main difference is in the external appearance only ; therefore it does not seem necessary to put any great stress upon this point.

*Meconopsis* is perhaps slightly more advanced than *Papaver*, and so is allotted the third place in the *Papaver* group ; the carpels are typically fewer than those of *Papaver*, also the flowers are frequently aggregated into a raceme, which, according to Wernham, indicates a step in advance of the solitary flower.

In the *Glaucium* group, *Sanguinaria* appears to be the most primitive type from many points of view. It has already been noted that the flowers have a more or less indefinite number of petals, a character that is seldom found naturally in the Papaveraceae, and this seems to be a link right back with the Ranalean types. Yet the gynaecium exhibits differentiation of carpels and the number is reduced to four, though the fertile carpels show the least contraction of any member of the Papaveraceae with a gynaecium of this type.

*Glaucium* appears to be the next in order ; this genus has a fixed number of petals. The gynaecium is of the same structure as that of *Sanguinaria*, but the fertile carpels are more compressed.

Although there is no tendency in *Glaucium* for the lateral strands in the fertile carpels to become inverted, the fertile carpels are much more inclosed by the expanded members than they are in *Sanguinaria*. *Chelidonium* is very similar, but in this genus the contracted carpels are mere ribs with the vascular system concentrated into one strand.

As has already been noted, *Eschscholtzia* appears to be the most highly evolved type in the Papaveroideae.

Taking all the characters of the Papaveroideae described in this communication into consideration, the most natural arrangement of the genera appears to be as follows :—

*Platystemon* group. (Flowers with three sepals, six petals, numerous stamens, and several to numerous normal free (ultimately) or fused carpels.)

- i. *Platystemon*.
- ii. *Platystigma*.
- iii. *Romneya*.

*Papaver* group. (Flowers with typically two sepals, four petals, numerous stamens, gynaecium an ovoid capsule exhibiting differentiation of carpels.)

- i. *Argemone*. (Sepals 2-3, petals 4-6.)
- ii. *Papaver*.
- iii. *Meconopsis*.

*Glaucium* group. (Flowers with two sepals, four petals, numerous stamens, gynaecium typically a long capsule exhibiting differentiation of carpels, but the number reduced to four.)

- i. *Sanguinaria*.
- ii. *Glaucium*.
- iii. *Chelidonium*.
- iv. *Macleaya*. (Petals absent.)
- v. *Eschscholtzia*.

There are many instances found while examining floral anatomy in detail which definitely show that in order to arrive at accurate conclusions, complete serial sections of the flower at every stage of growth must be studied. Examples to prove this point are found in many members of the Papaveraceae.

In the young flower-bud of *Glaucium flavum* the only indication as to the number of carpels lies in the four weak groups of vascular tissue in the floral axis. In the young gynaecium there is no indication of the carpel limits. The formation of the ovules is very late, for the other essential organs of the flower are perfectly developed long before the ovules make their appearance. The outstanding feature of the gynaecium in *Glaucium*, the 'false septum' of sponge-like tissue, is not developed until fertilization has taken place and the ovary has begun to enlarge.

In *Macleaya* branches of the main ribs in the expanded carpels do not appear until the fruit has reached semi-maturity.

At first sight, there is no indication in *Argemone*, *Papaver*, and *Meconopsis* of the pores which are ultimately disclosed for the purpose of seed-dispersal; the styler region or the stigmatic cap appears to be in continuity with the main part of the whole gynaecium-wall. A careful examination, however, will show that the valve-tips, though closely adpressed, are never actually united with those regions.

Notable alterations may take place in the positions and size of the floral organs—for instance, changes in the method of overlapping of sepals and petals as they become wider, and the spacing out of the staminal whorls as they become free from the axis. In *Papaver* the petals are smooth in a very young bud and only develop their characteristic wrinkles and folds as they rapidly increase in size immediately before the calyx splits.

The ovary of *Platystemon* again presents an instance where marked changes occur during development. The gynaecium resembles a vertically ribbed capsule surmounted by a cluster of slender stigmas, but soon after fertilization it splits up so that it has the appearance of an aetio of follicles. The internal structure also differs in the young fruit from that of an older one, for, as the fruit matures, each carpel becomes transversely divided into several compartments each of which contains a single seed.

Changes occur in the size and nature of the stigmas during the life of an *Eschscholtzia* flower, for when mature they resemble velvety plumes, but, as the fruit ripens, they wither away to small points surmounting the carpels.

The arrangement of the vascular strands at the base of the ovary in *Eschscholtzia* is a definite indication as to the number of carpels. This point is not taken into consideration by Saunders (22), who, apparently, did not examine the entire gynaecium from top to bottom, as she found the full complement of strands, which, however, usually do not appear for some little distance up the gynaecium; they are developed as branches of the primary vascular supplies to the gynaecium and are not the supplies of numerous carpels.

#### IV. HISTOLOGICAL FEATURES.

In dealing with the floral anatomy of the Papaveroideae, it is interesting to note the presence of secretory structures, which occur typically side by side with the vascular tissues. The substance secreted is latex, which may be contained in either sacs or tubes (vessels), and these in turn may be isolated or may run through the organs of the whole plant in conjunction with the vascular system. The latex differs in colour and density in each genus, and sometimes there is a marked difference between the species of the same genus, e.g. *Papaver*.

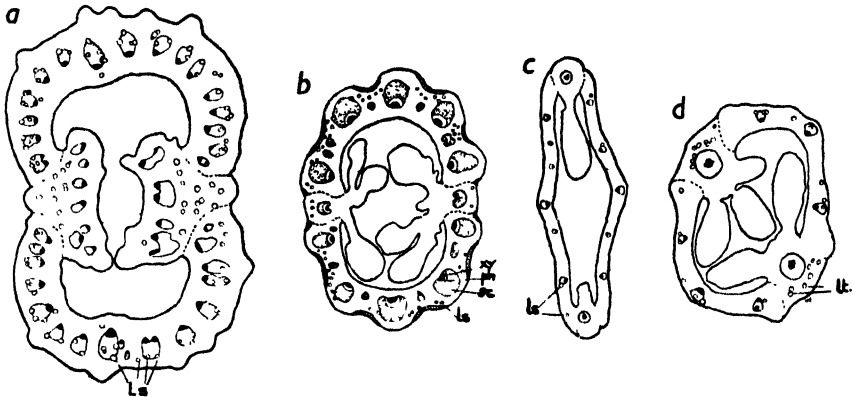


FIG. 30.

- a. T. S. of gynaeceum of *Glaucium flavum* Cr., showing latex sacs (*ls.*). ( $\times 15$ .)
- b. T. S. of gynaeceum of *Eschscholtzia californica* Cham., showing latex sacs (*ls.*), xylem (*xy.*), phloem (*ph.*), and sclerised tissue (*scl.*). ( $\times 15$ .)
- c. T. S. of gynaeceum of *Macleaya cordata* (Willd.) R. Br., showing latex sacs (*ls.*). ( $\times 15$ .)
- d. T. S. of gynaeceum of *Chelidonium majus* L., showing the distribution of latex tubes (*lt.*). ( $\times 35$ .)

The latex vessels which are present in *Papaver* spp. and many other members of the Papaveroideae are formed by the breaking down of the separating cell-walls, so that the cells become united to form tubes which branch and spread throughout the plant.

*Table to indicate the container and colour of the latex in various genera of the Papaveroideae.*

Genus.	Container.	Colour.
<i>Glaucium</i> . . . . .	Sacs.	Orange to colourless.
<i>Platystemon</i> . . . . .	Tubes.	Colourless.
<i>Papaver</i> . . . . .	Tubes.	Colourless to opaque.
<i>Sanguinaria</i> . . . . .	Sacs.	Bright red.
<i>Chelidonium</i> . . . . .	Tubes.	Orange.
<i>Macleaya</i> . . . . .	Sacs.	Orange.
<i>Eschscholtzia</i> . . . . .	Sacs.	Colourless to orange.

Transverse sections through the stem and gynaecium of an *Eschscholtzia* flower show dark patches of dense cells underneath the epidermis. These patches are always accompanied by one or several stomata with large air-spaces behind them (fig. 31, e).

It is tentatively suggested that the dark cells excrete volatile oils which escape through the stomata and vaporise immediately they come in contact with the atmosphere, or may even vaporise in the large air-spaces and are then exuded

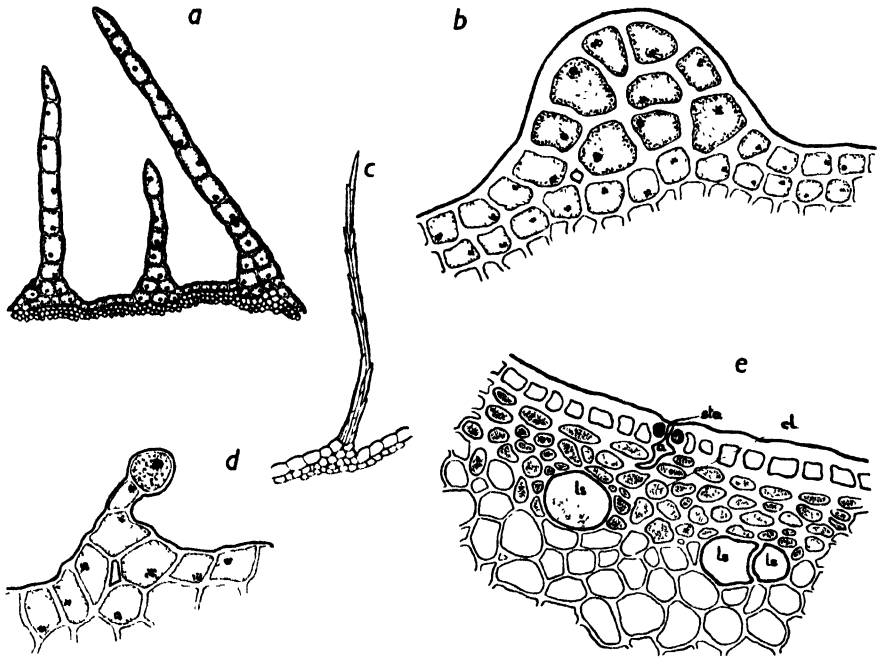


FIG. 31.

- a. Typical epidermal hairs of *Glaucium flavum* Cr. ( $\times 35$ .)
- b. Wart-like outgrowth on the gynaecium of *Glaucium flavum*. ( $\times 200$ .)
- c. Typical epidermal hair of *Papaver Rhoeas* L. ( $\times 20$ .)
- d. Glandular hair of *Glaucium flavum*. ( $\times 200$ .)
- e. Portion of the gynaecium of *Eschscholtzia californica*, showing stoma (sto.) with small densely filled cells behind (cl.), accompanied by latex sacs (ls.) (containing residue of latex), air-space (a.). ( $\times 200$ .)

from the plant in gaseous form. This seems fairly possible as there is no sign of an oily substance on the surface of the stem or gynaecium, and the plant as a whole, especially when young, tends to be aromatic when crushed; if this is so, the contents of the dark cells may be resin deposited on the evaporation of the oils.

It is interesting to note that the latex sacs lie, for the most part, between the vascular bundles and immediately behind these masses of small dark cells.

Therefore it may perhaps be assumed that the latex is secreted by the sacs, passed into the small cells where a deposit of resin is left, and the volatile oils collect in the large air-spaces and escape from the plant through the stomata.

Many members of the Papaveroideae are characterized by the numerous hairs which are scattered over the green parts of the plants. *Glaucium flavum* Cr. shows a wide variety in the formation of these hairs. There are simple uniseriate rows of cells (fig. 31, a), simple elongated epidermal cells, and a type, which, in the Papaveroideae, is peculiar to this genus, consisting of a row of simple cells terminated by one large spherical cell (fig. 31, d). (This type is comparable with those in *Pelargonium* (Geraniaceae). See diagrams in 'Studies in Floral Anatomy.—I' (3, p. 18).)

Solereder (25) remarks on the lack of glandular hairs in the Papaveraceae, but points out the hairs found by Léger (17) in *Glaucium flavum* which answer to the description of a 'typical glandular hair' \*.

Many specimens of *Glaucium flavum* were found with hairs of this type and in nearly every hair the spherical cell had densely protoplasmic contents. This is a point which strengthens the supposition that these hairs are glandular.

In discussing the hairy covering of *Glaucium flavum* it is also interesting to note that there occur on the surface of the ovary small wart-like projections; these are caused by outgrowths of the tissues situated just below the epidermal layer (fig. 31, b). The warts are very variable in size and shape, and the cells of the epidermis and those in the tissues of the wart possess dense protoplasm.

The green parts of certain members of the Papaveroideae are covered with a conspicuous grey-green bloom. This bloom is a wax layer or coating, and is most marked in such species as thrive in situations where they are frequently drenched with sea spray and even, at times, submerged, e.g. *Papaver somniferum* and *Glaucium flavum*; the wax layer, where it occurs, is very resistant and is especially so in these two plants.

## V. SUMMARY.

1. The floral anatomy of *Glaucium flavum* Cr. is described in detail and compared and contrasted with that of certain other members of the Papaveroideae, namely, *Plutystemon californicus* Benth., *Platystigma oreganum* Benth. & Hook. fil., *Romneya Coulteri* Harv., *Papaver Rhoeas* L., *Sanguinaria canadensis* L., *Chelidonium majus* L., *Macleania cordata* (Willd.) R. Br., *Eschscholtzia caespitosa* Benth.

2. It is shown that the gynaeceum in *Glaucium*, *Papaver*, &c., exhibits differentiation of carpels and presents a condition similar to that of the Cruciferae.

\* 'A typical glandular hair consists of two distinct portions, in addition to the base or foot, namely: first, a one- to several-celled stalk of varying length; and, secondly, the actual secretory organ or gland, which takes the form of a rounded head attached to the distal end of the stalk. The head may be unicellular as in *Pelargonium zonale* . . . ; or it may be divided into quadrants as in *Lamium* . . . ; or, finally, it may be composed of a large number of cells, as in *Sanguisorba carnea*.' (10, pp. 511-12.)

3. The gynaecaea of *Platystemon*, *Platystigma*, and *Romneya* are normal in structure.

4. *Eschscholtzia* stands apart from the other members of the Papaveroideae here described on account of its perigynous flowers ; and there is no indication as to the number of sepals, which are fused into a cap-like structure.

5. The flowers of the Papaveroideae, like the vegetative parts, are characterized by the secretion of latex, either in sacs or tubes, according to the genus ; several types of epidermal hairs and outgrowths are also present.

6. There are no true ' commissural ' stigmas in the Papaveroideae, for the alleged commissures are not fused fertile carpel-margins, but a separate series of contracted fertile carpels.

7. The gynaecaea of the Papaveroideae may be placed, roughly, in three groups :—

- i. Gynaecaea composed of several to numerous normally-formed carpels.
- ii. Gynaecaea composed of numerous carpels, but showing differentiation of carpels, i.e. alternate expanded sterile and contracted fertile carpels.
- iii. Gynaecaea exhibiting differentiation of carpels, but the number reduced to four.

8. It is suggested that *Platystemon*, on account of the Ranunculaceous composition of the gynaecium, is perhaps the most primitive type among the Papaveroideae, and that the genus may provide a definite connexion between the Ranales and the Rhoeadales.

9. There are many instances found while studying floral anatomy in detail which indicate that, in order to arrive at accurate conclusions, an examination must be made of complete serial sections of the flower in every stage of development.

The very grateful thanks of the writer are due to Dr. Helen Bancroft for suggesting the subject of this paper and for much invaluable advice during its preparation : to Mr. H. Gilbert Carter, Curator to the Cambridge Botanical Gardens ; Professor A. J. Eames, of Cornell University ; Sir Arthur W. Hill, Director of the Royal Botanic Gardens, Kew ; Professor Sir William Wright Smith, Regius Keeper of the Royal Botanical Garden, Edinburgh, for specimens of the various genera described ; to Professor R. S. Troup, Imperial Forestry Institute, and Professor J. A. S. Watson, School of Rural Economy, for the use of laboratory and apparatus.

The Imperial Forestry Institute,  
University of Oxford.

April 1934.



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## APPENDIX.

Since the foregoing paper was written, a further interpretation of the construction of the Cruciferous gynaeceum has been put forward by Spratt\*. This author upholds the bicarpellary theory, but is of opinion that the ovules are produced on the midribs and not on the margins of the carpels.

\* Spratt, E. R., 'The Gynoeceum of the Family Cruciferae', *Journ. Bot.* lxx, p. 308, 1932,

A quantitative study of geotropism and the development of the statolith apparatus throughout the life history of the wheat plant. By F. M. O. WAIGHT (Associate of University College, Reading). (Communicated by Dr. T. L. PRANKERD, F.L.S.)

(PLATE 5 and 3 Text-figures)

[Read 22 November 1934]

### INTRODUCTION.

It has already been shown (Prankerd, 1920) that the wheat haulm possesses two types of statocyte: (1) the smaller containing movable starch grains, and (2) the larger each with a movable crystal of calcium oxalate. The present work has been undertaken: (1) to follow the development of the statolith apparatus throughout the life of the wheat plant, (2) to determine the relative sensitivity to gravity at different stages of its life history with a view to ascertaining if or in how far they are correlated.

As in previous work (Prankerd 1929, p. 317) the presentation time has been used as a means of measuring geotropic sensitivity, and is defined as the shortest period necessary under specified conditions to produce a movement of not usually more than  $5^\circ$  in about 80 per cent. of the plants. The latent time is the period elapsing between the beginning of stimulation and the first visible indication of response.

Most of the work has been carried out on 'Standard Red' wheat grown in experimental plots, and also in pots both in the greenhouse and in the open. This was supplemented by work on wheat from the field where the variety was not known, but no difference in behaviour was found. Much of the work was done in summer, and the range of temperature during experiments was  $16^\circ$ – $20^\circ$  C., whether in the unheated greenhouse or in the open. During winter months it was found necessary to perform the experiments on pot plants in a research greenhouse heated to  $20^\circ \pm 1^\circ$  C. The plants were kept in the greenhouse only for the duration of the experiment, as the conditions, particularly the high humidity, were not suitable for the healthy growth of wheat. Plants were grown in pots as they could be handled more easily, and it was found possible to bring them to maturity; but as sometimes the ears were poor, and fewer nodes were developed, the experiments on these plants were only used to verify the methods employed on those growing in the open. Stimulation was effected with plants grown in pots by placing these and therefore the

haulms horizontally. Haulms growing in a plot were bent horizontally and kept in that position by means of bast attached to the ground. When the haulms were replaced in the vertical position, it was often necessary to support them to counteract a sag due to the previous bending. This sag could be avoided in pot plants by supporting the haulm while in the horizontal position.

For cytological work the material was fixed in acetic alcohol or 70 per cent. spirit, both of which gave satisfactory results.

The life history of the wheat plant falls naturally into the following stages, which have been sub-divided as follows :—

I. *Grain stage*, i.e., the ripened fruit till germination.

II. *Seedling stage*.

A. From the emergence of the coleoptile till it is 0.5 cm. in length.

B. Coleoptile from 0.5–1.0 cm. (approx.).

C. Coleoptile from about 1.0 cm. to the time of splitting, when the average height is 2.25 cm.

III. *Leafy or adolescent stage*. The habit is tufted, and the visible part of the shoot consists of the developing leaves with their sheaths rolled round one another. The undeveloped stem has no internodes and is enclosed by the youngest leaf.

A. From the splitting of the coleoptile, and the emergence of the first foliage leaf to the appearance of the second foliage leaf and withering of the coleoptile.

B. From the appearance of the second foliage leaf to that of the last.

C. During the development of the last foliage leaf.

IV. *Mature stage*, including the sub-mature or development of the internodes (the 'shooting' of the plant, Percival 1920, p. 82).

A. From the formation of the first thickened leaf-sheath just above the node to the opening of the flowers.

B. Flowering.

C. Fruiting, i.e., from the withering of the flowers to the dispersal of the grain and the death of the haulm.

The following abbreviations are used :—

P.S.=Period of stimulation.

P.T.=Presentation time.

L.T.=Latent time.

I. *Grain stage*.

Cytological examination shows that no starch is present in the embryo, and naturally no curvature can take place,

## II. Seedling stage.

When the coleoptiles are in stage A they are scarcely sufficiently free from the fruit to move in response to gravity. The following experiment was performed to ascertain the geotropic power of young coleoptiles. Seeds were soaked for forty hours, then planted in damp cotton wool and placed in the dark. After fifty-five hours, when germination had commenced, they were placed with the coleoptiles at different angles and still kept in the dark. Forty-eight hours later all the coleoptiles in stage A were curving at various angles, while those in stage B had reached the vertical. It seems, therefore, that the coleoptiles are sensitive to gravity from the first, but the sensitivity cannot be easily measured till they are 0.5–0.6 cm. in length.

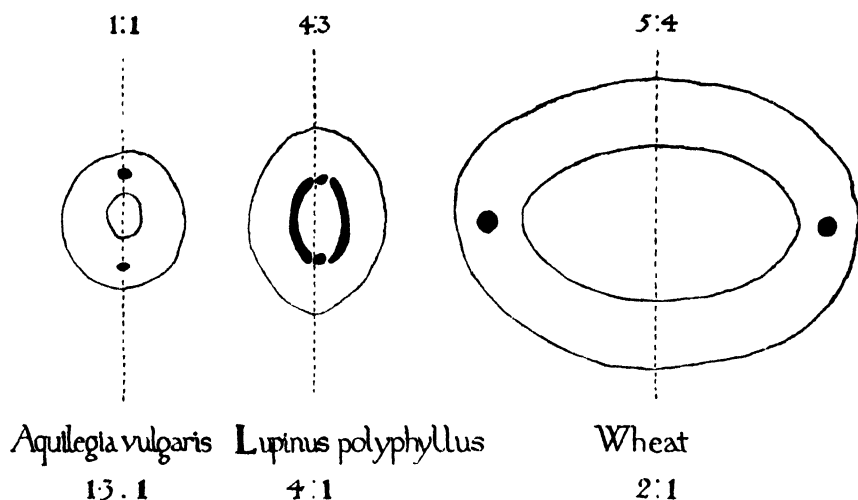


FIG. 1.—Transverse sections drawn to scale of three seedlings in the region of geotropic curvature. The dotted line in each case represents the plane of quicker perception and reaction (i.e. the cotyledonary for the dicotyledons and the inter-vascular bundle for the monocotyledon). The figures above the sections are the ratios of the lengths of two axes; the figures below the sections are the corresponding ratios of the presentation times.

During stages B and C seedlings are most reactive to the stimulus of light. The difficulty of light curvature was overcome during experimental work by enclosing the young plants in cylinders of white paper, the method employed by Bach (1907). In stimulating seedlings in stages B and C the plane of stimulation was found to be an important factor. The coleoptile of wheat is elliptical in transverse section, and contains two bundles in the plane of the longer diameter (fig. 1). It was found that shoots stimulated in this plane, here termed the vascular, require twice the P.T., and do not react so quickly as

those stimulated in the plane at right angles to this, i.e. the intervascular. The details of experiments demonstrating this are given in the following table :—

TABLE I.—*Seedling stages B and C.*

(a) Stimulated in vascular plane.

Height in cm.	Period of stimulation in minutes.	Angle of curvature.	L.T. in minutes.
1.4	20	5°	80
1.2	20	5°	80
0.8	20	5°	80
2.0	20	—	—
3.0	15	4°	70
3.5	15	—	—
3.2	10	—	—
2.5	10	—	—
2.0	10	—	—
1.5	10	—	—

P.T.=20 minutes ; L.T.=80 minutes.

(b) Stimulated in intervascular plane.

2.5	10	7°	55
3.7	10	5°	55
2.5	10	5°	60
1.5	10	5°	70
1.0	10	5°	90
3.4	10	—	—
1.0	10	—	—
2.4	8	5°	80
1.5	8	5°	70
2.8	8	—	—
1.8	8	—	—

P.T.=10 minutes ; L.T.=66 minutes.

This phenomenon was first described by Brain (1926) for certain Dicotyledons, and termed physiological zygomorphy (pp. 651 & 656). She found that these seedlings were always more sensitive to gravity when placed horizontally so that the cotyledonary plane was vertical. An instructive comparison can be instituted between the structure and behaviour of wheat with that of *Aquilegia vulgaris* and *Lupinus polyphyllus*. For this purpose the cross-sections of these seedlings are reproduced in fig. 2 from text-fig. 2a of Brain's paper. *Aquilegia* forms a striking contrast in that the cotyledonary plane is also the vascular plane, i.e. the two bundles occur in the plane of quicker reaction, but in wheat they run in the less sensitive plane. The cross-section of *Aquilegia* is almost radial, but that of *Lupinus*, like wheat, is elliptical. Again, however, we have an interesting difference in behaviour, for while this seedling is most reactive in the plane of the major axis, which also contains two small bundles, the reverse is the case in the wheat. In other words, the quicker plane for *Aquilegia* is vascular and for *Lupinus* contains the major axis ; while in wheat the quicker plane is non-vascular and contains the shorter axis. It seems probable therefore that the differential irritability is not causally

connected either with vascular structure or with the relation of the axes of symmetry to the plane of stimulation.

With the emergence of the shoot starch appears for the first time in the embryo (fig. 2). Nearly every cell of the ground tissue in the coleoptile is starch-containing, but so closely are the grains packed that it is difficult to say whether they are free or embedded in whole or in part. At stage B conditions are similar quite at the apex, but lower down the starch content decreases, though to a less extent in the bundle sheaths. Here and sometimes in the ground tissue many of the grains are free to fall, and are consequently found on the physically lower walls of the cells. Nearer the base, and particularly around the bundles, more typical statocytes occur, i.e. practically all

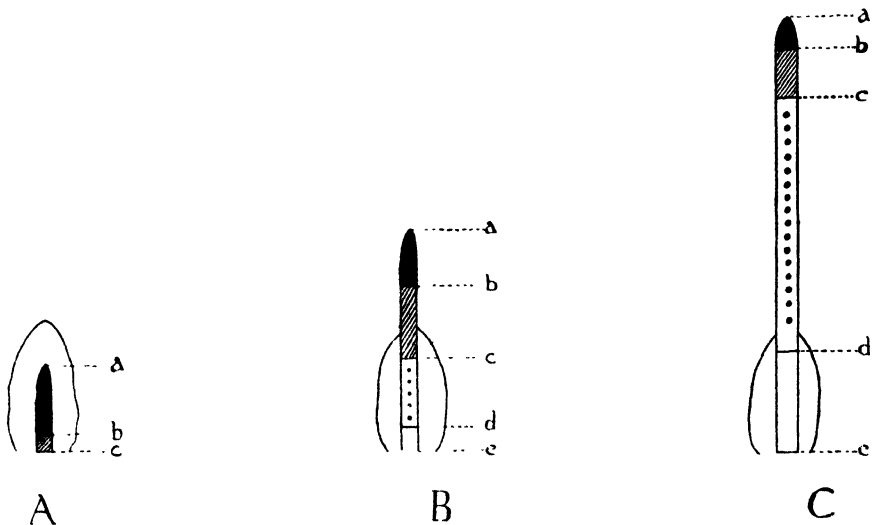


FIG. 2.—Diagrammatic representation of the distribution of starch and statoliths in the three substages (p. 226) of coleoptile development. *a-b*, dense starch; *b-c*, starch concentrating round bundles; *c-d*, statoliths and embedded starch; *d-e*, statoliths and starch disappearing.

the starch grains are found on the cell walls which were physically lower before fixation. At stage C starch still remains dense at the apex, gradually becoming less passing downwards until all embedded starch dies out, and only statolith starch is found in the bundle sheaths. At the base starch and statoliths have mostly disappeared.

The phenomenon of physiological zygomorphy has recently been harmonized by Hawker (1932) with the statolith theory of graviperception. She found that in this type of seedling the statocytes were elongated tangentially, so that sometimes the shorter axis lay in the plane of greater irritability, while in a few the longer axis was so placed. Hence in the former a larger area of sensitive protoplasmic surface would be exposed to the impact of the falling grains, which would reach it in a shorter time.

Careful observation of the statocytes in the coleoptile of the wheat seedling revealed that most of those occurring in the bundle sheaths were ellipsoidal, and the majority were situated so that the major axis lay in the vascular plane. The ratio of the number of those with their minor axis to the number of those with their major axes in the intervascular plane is 4·7 : 1 ; and the ratio of the lengths of the axes is 1·5 : 1. Thus the ratio of the surface stimulated in the intervascular plane to that stimulated in the vascular plane is

$$[(4\cdot7 \times 1\cdot5) + (1 \times 1)] : [(4\cdot7 \times 1) + (1 \times 1\cdot5)]$$

i.e. 8·05 : 6·2.

Multiplying this by the ratio of the relative time of fall of the statoliths, we have what Hawker (p. 136) termed 'statolith efficiency' as

$$8\cdot05 \times 1\cdot5 : 6\cdot2 \times 1 \quad \text{or} \quad 1\cdot9 : 1.$$

Accordingly, only half the intensity of stimulation (=P.T.) required for the vascular plane should be needed for the intervascular plane, which is precisely what was found independently by experiment (Table I).

### III. Leafy stage.

The transition as regards external morphology and geotropism from the seedling to the leafy stage is a rapid one. As the first leaf emerges from the coleoptile (substage A, p. 226), the response to gravity diminishes, though the intervascular plane remains more sensitive than the vascular, and in the same ratio. The P.T. for the intervascular plane increases from ten to thirty minutes and for the vascular plane from twenty to sixty minutes (Table II).

TABLE II.—*Leafy stage A.*

Height in cm.	Period of stimulation in minutes.	Angle of curvature.	L.T. in hours.
2·5	60	10°	2·0
2·0	60	10°	3·0
2·7	60	5°	2·5
2·1	60	5°	3·0
1·7	60	5°	2·0
2·6	60	—	—
2·1	60	—	—
1·6	50	—	—
2·3	30	—	—
2·2	30	—	—

P.T. = 1 hour ; L.T. = 2·5 hours.

(b) Stimulated in intervascular plane.

2·1	30	5°	2·0
2·0	30	5°	2·0
1·9	30	5°	2·0
1·8	30	5°	2·0
1·3	30	5°	2·0
1·7	30	5°	3·0
1·5	30	—	—
1·5	30	—	—
2·0	25	—	—

P.T. = 30 minutes ; L.T. = 2 hours.

As the first leaf matures, the P.T. increases still further in both planes, but more rapidly in the intervacular. With the appearance of the second leaf and the gradual withering of the coleoptile, the region of curvature moves to the leaf sheaths. Radial symmetry prevails in this region, and the P.T. now reaches 120 minutes (Table IV), irrespective of the plane of stimulation. During the subsequent period of leaf development (substage B), the P.T. remains constant at this value, but at substage C, with the development of the last leaf and the beginning of the elongation of the first internode, it rapidly diminishes to 60 minutes (Table IV). The L.T. varies in the same direction as the P.T., but not to the same extent as will be seen from the Tables.

TABLE III.—*Leafy stage B.*

The letters V or I after the figures in the first column indicate that the seedling was placed in the vascular or intervacular plane respectively.

Height in cm.	P.S. in minutes.	Angle of curvature.	L.T. in hours.
9.5 (I)	120	5°	4
10.0 (V)	120	5°	4
12.0 (V)	120	5°	4
10.2 (V)	120	4°	4
10.5 (V)	120	3°	4
6.7 (I)	120	2°	4
8.5 (I)	120	—	—
10.0 (V)	120	—	—

TABLE IV.—*Leafy stage C.*

Height in cm.	P.S. in minutes.	Angle of curvature.	L.T. in hours.
10.0	60	7°	4.5
11.0	60	5°	3.3
14.0	60	5°	4.0
11.0	60	5°	4.0
11.0	60	5°	4.0
5.4	60	5°	4.0
5.4	60	5°	4.0
13.0	60	—	—
11.0	60	—	—
11.0	60	—	—

With the emergence of the first leaf, both statoliths and embedded starch rapidly disappear from the coleoptile. In the case of the statocytes, stages have been traced where only some of the starch grains are free to fall, the others having become embedded in the cytoplasm. Hence an absorption of the grains as such evidently takes place before their ultimate solution. Both embedded and statolith starch appear throughout the leafy stage, but never to the same extent as in the coleoptile. Some statocytes with a few statoliths are usually to be found in the bundle sheath, and there is sometimes a little embedded starch in the ground tissue. The latter, however, is inconstant in appearance and



often absent except at the base of the leaf, where the cells are packed with starch grains, much as in the very early coleoptile stage. As the last leaf develops, much more typical statocytes occur in the bundle sheaths towards the bases of the leaves. At the close of this stage the first characteristic swelling of the leaf sheath just above the node begins to form, and the starch statocytes in this region are restricted to little groups internal to the bundles as described in the next section.

#### IV. *Mature stage.*

Externally this stage obviously falls into three divisions: (1) development of the stem, (2) flowering, (3) fruiting. Response to gravity, while corresponding to these divisions, cannot be sharply tabulated, as it does not remain constant

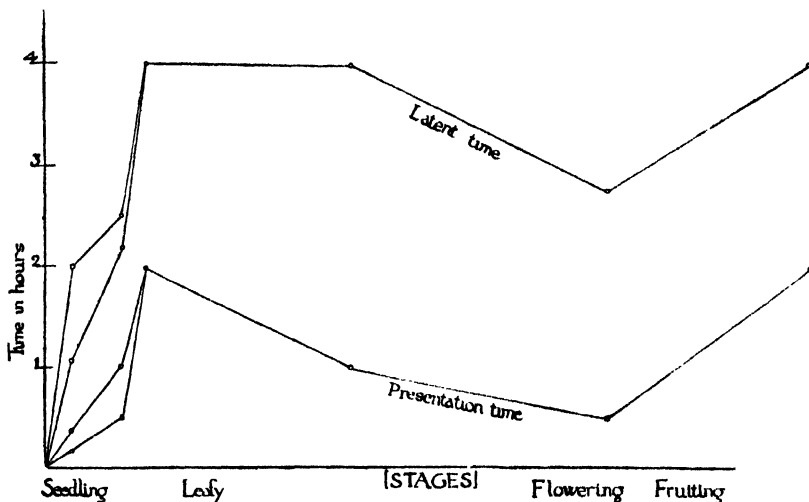


FIG. 3.—Graviscritps of the life history of the wheat plant.

for any length of time. Rising gradually with the growth of the haulm and the development of the ear, it reaches a maximum for this stage during flowering and then falls steadily while the fruit is forming until the plant dies. The experiments recorded in Table V illustrate this, showing that the decrease in the P.T. begun at the end of the leafy stage is continued till it reaches a minimum of thirty minutes while the ear is in flower. As the grains ripen it continues to increase till even five hours may or may not yield a response, and finally as the last grains are falling, continuous stimulation fails to produce any movement.

At the beginning of this stage, just at the base of the lengthening internode most of the cells of the ground tissue are packed with starch. As in the very young coleoptile it is impossible to determine whether the grains are embedded or free, but in either case they soon disappear. As the internodes lengthen, the leaf sheaths swell just above their attachment to the stem, and the whole

of the ground tissue in this region is developed as statenchyma. Small patches of cells adaxial to the bundles produce movable starch grains, while practically all other cells of the ground tissue are each seen to possess a crystal or crystal aggregate, which is very easily movable within the cell (Pl. 5). This condition is constant until just before the death of the haulm, when the starch disappears and the crystals remain.

TABLE V.—*Mature stage.*

(The height recorded in the second column denotes the distance between the ligule of the youngest leaf and soil level, and the angle of curvature is that of the youngest leaf sheath.)

Substage.	Height in cm.	P.S. in minutes.	Angle of curvature.	L.T. in hours.
(A 1) Ear shooting .....	37.0	60	5°	3.5
	34.5	60	5°	3.5
	37.5	60	5°	3.0
	37.5	50	5°	2.5
	32.0	45	5°	4.0
	37.0	45	—	—
(A 2) Just before flowering ....	38.5	45	5°	2.5
	45.0	45	3°	4.0
(B) Flowering .....	50.0	45	3°	4.0
	57.0	30	5°	3.0
	59.0	30	5°	2.75
	58.0	30	5°	2.75
	78.0	30	4°	3.0
	54.0	30	4°	2.5
	60.0	30	3°	2.75
	58.0	30	2°	2.75
	57.0	30	—	—
	54.0	30	—	—
	52.0	30	—	—
	90.0	20	5°	3.0
	47.0	20	—	—
	34.0	20	—	—
(C 1) Directly after flowering ..	46.0	90	5°	4.0
	42.0	90	5°	3.0
	47.0	60	5°	4.5
	36.0	60	—	—
(C 2) Fruiting.....	47.0	120	5°	3.25
	50.0	150	5°	4.5
	50.0	150	5°	4.0
	50.0	150	5°	4.0
	49.0	150	5°	4.0
	48.0	150	—	—
	58.0	150	—	—
	59.0	150	—	—
	58.0	240	4°	5.5
	59.0	300	5°	5.5
	59.0	No response for continuous stimulation.		

Table VI. is a summary of the sensitivity to gravity (expressed as the reciprocal of the P.T. for each stage), and the corresponding appearance of statoliths and embedded starch; while the graviscritps (Pranker, 1929, p. 318) for the life history of the wheat plant are given in fig. 3 (p. 232).

TABLE VI.

Stage.	Relative sensitivity.	Statocytes.	Embedded starch.
Grain .....	.....	None.	None in embryo.
Seedling .....	(A) Response to continuous stimulation.	Forming.	Much.
	(B) } 1000 or 500	Well-developed starch statoliths.	Much.
	(C) } according to plane.		Less.
Adolescent ....	(A) 333 or 167 according to plane.	Ill developed.	Decreasing.
	(B) 84.	Traces.	Little.
	(C) 167.	Increasing.	Much at bases of leaves and elongating internode.
Mature .....	(A) 200 } (B) 333. } (C) Rising.	Well-developed starch and crystal statoliths. .....	None.

## DISCUSSION.

We have now before us, it is believed for the first time, the complete life history of a single plant as regards geotropic activity and the synchronous development of movable bodies within the cell.

In the first place, it may be noted that some points in previous work have been confirmed with perhaps fresh emphasis. As in the ferns (Waight 1923, Pranker 1929) it is established that the degree of sensitivity is associated with the stage of development and not the length of the part concerned. And, similarly, the period elapsing before response is affected by the stage and not the age of the organ, though to a less extent than presentation time.

Tröndle (1910, pp. 225 & 227) working with centrifugal force asserted that latent time ('Reaktionzeit') equalled presentation time plus a constant for different values of  $g$ ; and, calculating from Pekelharing's\* data, gave  $K=45$  for *Avena sativa*. He, however, took no account of the plane in which the shoots were stimulated, which is shown here to be a factor of great importance. From Table I it will be seen that the value of Tröndle's constant (i.e. L.T.-P.T.) for wheat seedlings under gravity is 55 or 60, according to the plane of stimulation—a quantity sufficiently near his for the oat to be perhaps of some interest.

\* Presumably Pekelharing's figures refer to the seedling stage of the oat, but I have been unable to obtain the original dissertation to verify this.

The constant may well be a specific character (*cf.* Prankerd, 1929), and therefore of significance, but the many factors influencing *graviperception* must be borne in mind in its calculation.

The above are interesting points of detail, but the outstanding result of the work is the quantitative correlation of *graviperception* and reaction with the statolith apparatus, and of both with the stages passed through in the life history of the plant. Remarkable instances of association between geotropic sensitivity and the presence of statoliths have frequently been pointed out, and used as an argument in support of their causal connexion (Darwin, 1906; Haberlandt, 1914). A distinct advance was made when a *quantitative* relation was demonstrated between the two phenomena in a fern frond and a number of seedlings (Prankerd, 1922; Hawker, 1932), and the present work shows this to hold good in general for the successive phases of a complete life history. Starting with the grain, we find no trace of statoliths in the quiescent embryo; but they appear just at the time (first stage of germination) and in the place (coleoptile) of gravitational activity. The presentation time is now at its minimum (ten minutes), and the statolith apparatus is very well developed. All the cells of the ground tissue are potential statocytes, and these are always developed round the bundles. In addition to its obvious function of protection, the coleoptile may well be regarded as a definite sense organ. During the period of leaf development, the P.T. is at its maximum for any active phase, and statoliths are very feebly developed. As the haulm grows the P.T. again decreases, while very well-defined statocyte tissue is developed exactly in the regions of geotropic curvature. These are the swollen leaf bases which form another type of sense organ already designated as such (Prankerd, 1914). While the grain is filling, there is obviously a great drain on the plastic material of the plant, as shown by the complete absence of embedded starch in any part of the haulm. Under such conditions it is surely remarkable that starch-containing cells are found at all, though where this is so, as we have seen, every grain is movable. With regard to the two types of statolith, the suggestion has been made 'that in the course of evolution the wheat plant may be substituting a body, metabolically harmful, but heavier and therefore quicker and better as a statolith, for the usual starch grain, which is required as nutrient for the ear' (Prankerd 1920, p. 151).

After flowering the P.T. increases rapidly, and as geotropic sensitivity ceases the starch statoliths are absorbed, never to reappear again. Since the plant is an annual, continuing its existence in the form of a fruit, the waste products thrown down as calcium oxalate are completely eliminated.

These facts would seem to be in accordance with the biological needs of the plant. During the seedling stage an erect position is secured by the quick response of the little shoot to gravity. As soon as the foliage leaves have emerged and droop in all directions, the 'pseudo'-stem formed by their leaf sheaths is less likely to be blown down, and an erect position is, moreover, of less importance. Correlated apparently with this are the perceptive and reactive

powers, which are at their minima for gravity during this stage. But when the internodes are elongating, 'lodging' takes place all too easily, and with serious consequences. Coincidentally, reactive power to gravity increases, rising to a maximum for this stage at flowering time, when an erect position is almost a necessity. During the ripening of the ear, geotropic power wanes as the vertical position becomes of less and less importance, and ceases at fruit dispersal.

Even if this should not be an entirely correct reading of this aspect of the life of the plant, there can be no question as to the close association in time and space between geotropic sensitivity and the development of the statolith apparatus. Further, this correlation is approximately quantitative, and corresponds with the various stages passed through by the wheat plant in the course of its life history. Fresh evidence is thus afforded for the truth of the statolith theory of geotropism.

#### SUMMARY.

1. The intensity of the response to gravity has been worked out for each stage in the life history of the plant. It is at its maximum in the seedling stage, falls to a minimum during the leaf formation, rises again up to flowering time, and dies out with fruit formation.

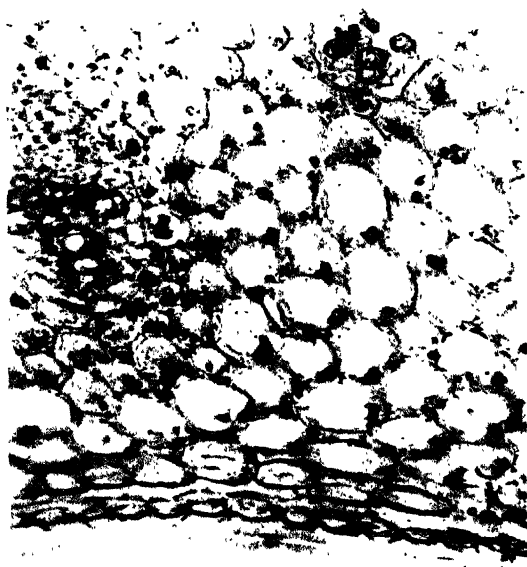
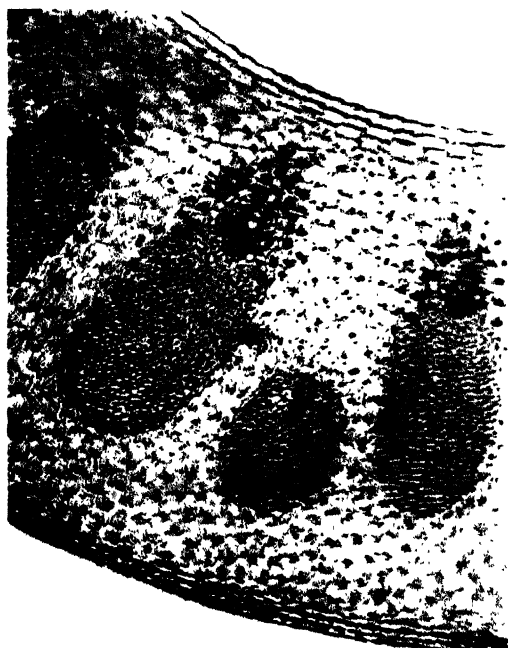
2. The production of statocyte tissue is correlated with geotropic activity in quantity, time, and space. It is poorly represented during the leafy stage, and attains its greatest development in the coleoptile and the swollen bases of the leaf sheaths, both of which are regarded as definite sense organs.

3. The phenomenon of physiological zygomorphy described for certain Dicotyledonous seedlings is shown to hold good for a Monocotyledon. It is probably not directly affected by the symmetry of the axis or that of the vascular tissue, but seems to be causally connected with the structure of the statocytes.

This work was carried out under Dr. Prankerd's direction. My grateful thanks are due to her for the help and advice she has so willingly given me.

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2.

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DEVELOPMENT OF THE WHEAT PLANT



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## EXPLANATION OF PLATE 5.

Fig. 1. Part of a transverse section across the swollen leaf-sheath of wheat just above the node (*cf.* Prankerd, 1920, fig. 1).

The section is bounded on each side by epidermis and collenchyma, and the bundles are accompanied by large abaxial strands of sclerenchyma. Note the starch statocytes occurring adaxially to the bundles, and the whole of the rest of the ground tissue developed as crystal statenchyma. ( $\times$  c. 60.)

Fig. 2. Part of the ground tissue more highly magnified. Note the single crystal on the basal wall of each cell. ( $\times$  c. 150.)





A sketch of the geography and botany of Tibet, being materials for a flora of that country. By Capt. F. KINGDON WARD, B.A., F.L.S.

(With 2 sketch-maps)

[Read 10 May 1934]

### I. BOUNDARIES AND AREA.

The boundaries of a country such as Tibet are necessarily uncertain and fluid. Do we mean Tibet as a geographical or as a political unit? Nor is it easier to define the one than the other. However, it is customary in compiling floras of unit areas to rely on man-made boundaries, since these *can* be rigorously defined. Yet since they are made by man, they can be, and from time to time are, altered by man. Political frontiers rarely coincide with geographical boundaries; but no Tibetan would agree with an Englishman as to what constitutes a geographical frontier—which fact rather vitiates the use of the term ‘natural frontier’. We may agree, therefore, that all frontiers are arbitrary, and leave it at that.

For the purpose of this study I have taken a generous, but not, I think, unduly generous view, of Tibet as a political unit. The Lhasa government may not control the entire area, or at any rate its control may not be equally rigid all over; on the other hand, in certain directions it may extend even beyond the boundaries I have laid down. But, even so, ethnographic Tibet extends far beyond political Tibet; ethnographic Tibet not under the Lhasa government has been ignored.

The frontiers of Tibet as here recognized differ but little from those of that great authority, Sir Charles Bell, K.C.I.E., C.M.G. (see ‘Tibet Past and Present’), and may be regarded as reasonable. Tibet then is bounded on the north by the Kun Lung range and its off-shoot the Altyn Tagh, which embraces Tsaidam; on the east by the Chinese provinces of Kansu, Szechuan, and Yunnan, in the neighbourhood of the one hundred and second meridian; on the south by the mountainous parts of north-western Yunnan, far northern Burma, Assam, Bhutan, Sikkim, Nepal, and Kumaon; and on the west by Kashmir, Ladakh, and Chinese Turkestan. From east to west the longest measurement across Tibet is about 1300 miles, from north to south 800 miles. The superficial area is about 750,000 square miles, or nearly ten times as large as Great Britain. The average elevation of the whole may be taken as from 14,000 to 16,000 feet, which is a conservative estimate, though, like all averages, it is apt to be misleading.

European travellers have penetrated into all parts of Tibet; nevertheless, great areas still remain unexplored. The systematic collecting of plants has

been carried on in only a few widely scattered localities, though most travellers have brought back small collections. The records of these are also scattered, and our knowledge of the Tibetan flora is still very inadequate. This seems a fitting opportunity, therefore, both to summarize our knowledge and to attempt some ordered picture of the country as a whole, with its botanical regions and relationships\*.

Although the flora of Tibet is usually assigned *en bloc* to the Central Asian region of Drude, yet, having regard to the whole country, we find that two other floral regions encroach on it and have made their influence felt. These are (1) the Indo-Malayan region, along the southern border, and (2) the Eastern Asiatic region along the eastern border. All three floras meet in the mountainous south-eastern part of the country, and all three have at one time or another been in close contact, owing to the advance and retreat of the ice here. The net result has been that from the three floras has crystalized on the mountains (as opposed to the plateau) a flora with many endemic species and small genera related to all three. This flora I have previously called Sino-Himalayan.

The type of vegetation—whether forest, deciduous or evergreen, parkland, grassland, or semi-desert—met with in any region depends on a number of factors, but mainly on the absolute rainfall and its seasonal distribution and the relative humidity of the atmosphere. So is it with the vegetation of Tibet. However, it is usual to consider the vegetation of a country in its broader aspect, in relation to *one* factor only, namely, absolute rainfall. A truer criterion would be the relative atmospheric humidity, of which the total annual rainfall gives only a rough indication. But rainfall is more easily measured.

Unfortunately, there are no rainfall records for Tibet; we must depend on the scattered and uncoordinated observations of travellers, and largely on guesswork. Piecing these together, it is nevertheless possible to arrive at certain general conclusions. The main vegetative divisions of Tibet correspond closely with the physical features of the country, and also serve to distinguish the climatic regions. Thus, as regards precipitation, we may roughly divide Tibet as follows:—

<i>Rainfall.</i>	<i>Region.</i>
0–10 inches . . . .	Chang Tang and Tsaidam (north-central, western, and north-eastern Tibet).
10–20 inches . . . .	Outer plateau (south-central and central-eastern Tibet).
20–30 inches . . . .	Upper gorge country (south-eastern Tibet). Grassland plateau (eastern and north-eastern Tibet).
Over 30 inches . .	Lower gorge country (south-eastern Tibet); Chinese Tibet.

\* The last attempt at a comprehensive account of the Tibetan flora was that by W. B. Hemslay and H. H. W. Pearson in the 'Journal of the Linnean Society, Botany', vol. xxxv, 1902. I have found the information given there invaluable.

Over the greater part of Tibet the greatest rainfall occurs during the summer, during the progress of the south-west monsoon; spring, too, is a wet season.

The Tibetan flora is necessarily almost entirely an alpine flora; three-quarters of the country, being elevated more than 13,000 to 14,000 feet, possesses no other. Only in the river gorge country does it cease to predominate.

Where the great Tibetan rivers traverse the outer plateau and upper gorge country a special arid region flora is developed between 8,000 and 12,000 feet altitude; while in the Tsangpo valley from Lhasa eastwards, there is much blown sand, which supports a characteristic scrub flora. But local plant associations, dependent upon special conditions, are, of course, numerous.

As regards the geographical divisions of Tibet, their botanical equivalents are as follows:—

The Chang Tang, Tsaidam, and Outer Plateau have been regarded as belonging exclusively to the Central Asian floral region.

The upper gorge country has a flora partly Central Asian, partly Eastern Asiatic, partly Himalayan, and partly indigenous.

The lower gorge country has a strong admixture of Indo-Malayan, Himalayan, and Eastern Asiatic species; while most of Chinese Tibet and the Himalayan region (regarded by Drude, at high levels, as a westward prolongation of the Eastern Asiatic flora) is occupied by the flora I have hitherto called Sino-Himalayan.

In the river gorge country differences of altitude amounting to 10,000 or 12,000 feet are not uncommon; and in extreme instances they may reach 15,000 feet; the valleys being 5000 to 8000 feet high, the peaks 17,000 to 23,000 feet high.

On the plateau there are no such contrasts; valleys and ranges hardly differ by so much as 5,000 feet.

## II. THE GEOGRAPHY OF TIBET IN RELATION TO ITS FLORA.

The physical geography of Tibet is comparatively simple. Tibet is a lofty plateau, oval or pear-shaped, rimmed by great ranges of even loftier mountains—the Kun Lun to the north, the Great Himalayan range to the south. The plateau itself is traversed by other ranges, diverging from the narrow western end.

Throughout Cretaceous time the plateau was beneath the sea called Tethys, nor did it become dry land till long after the dawn of the Tertiary period. Thus Tibet is, by the geological time-scale, a new land. Ever since this vast plateau rose to eminence, the forces of nature have been violently destroying and reshaping it. As a result, we can clearly distinguish three divisions of the plateau.

*Great Plateau.*

(I) First, the Chang Tang (literally 'northern plain') or great plateau. The drainage is internal, short rivers ending in lakes which, having no outlet, are salt or brackish. The climate is very severe, and the Chang Tang is, botanically, almost a desert. It is uninhabited. Tsaidam, though 6,000 feet lower, is included here.

*Outer Plateau.*

(II) Secondly, the outer plateau. Here the water is beginning to flow outwards, till eventually it reaches the sea \*. So gradually does the Chang Tang slope towards the south-east that the watershed between the internal and external drainage is imperceptible. As the rivers increase in size, the country becomes more fertile, till finally it shelves down to the river gorge country. South of the Chang Tang is the mountainous area which Sven Hedin traced for 600 miles between the great plateau and the Tsangpo valley. Southwards, therefore, the transition is more abrupt. Most of the Tibetan towns—Lhasa, Gyantse, Shigatse, Tsetang—are situated on the outer plateau. There are a few small fresh-water lakes, and numerous rivers flowing in wide shallow east-west valleys. The climate is much less severe than that of the great plateau, and there is a considerable alpine flora. Trees are confined to the water courses. In the south the outer plateau is a gravel country, in the east it is a grassland country.

(III) Thirdly, the river gorge country. Here the streams, which rise on the low rim of the saucer-shaped Chang Tang and flow for hundreds of miles across the outer plateau in comparatively broad shallow valleys, begin

\* The rivers which flow outwards from the northern rim of the plateau flow only into the Central Asian depression, the Tarim basin. The Indus and Sutlej flow westwards. Five great rivers flow eastwards.

## EXPLANATION OF MAP I (p. 243).

*The geographical and botanical divisions of Tibet.*

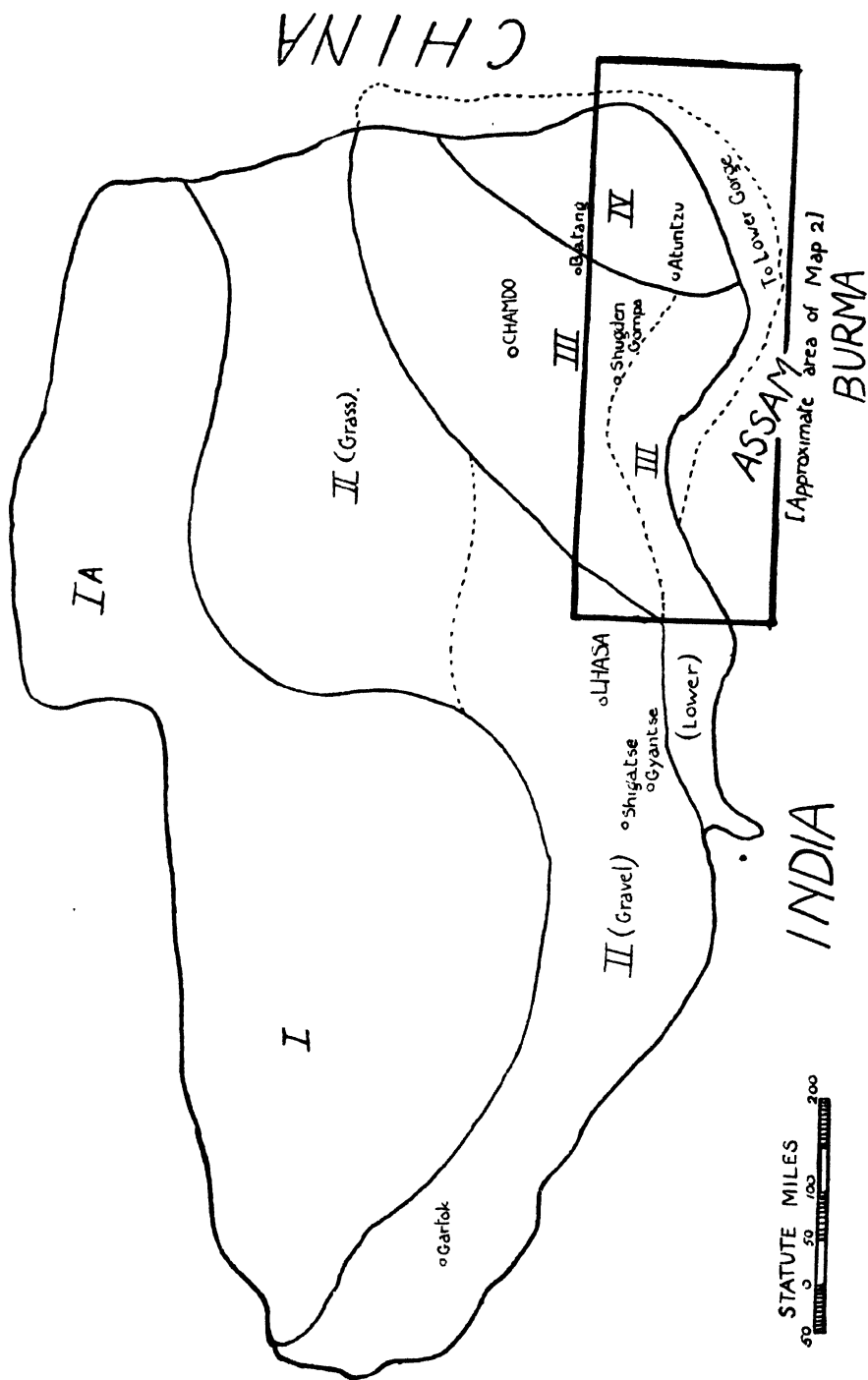
- |  |                          |
|--|--------------------------|
| I. Chang Tang.                               | } Sino-Himalayan Region. |
| IA. Tsaidam.                                 |                          |
| II. Outer Plateau. (Grassland and gravel.)   |                          |
| III. River Gorge Country. (Upper and lower.) |                          |
| IV. Chinese Tibet.                           |                          |

The Outer Plateau is divisible into two parts: gravel lands in the south and west, grass lands in the north and east.

The river gorge country is divided into upper and lower. Part of the lower gorge country lies outside Tibet proper.

The Sino-Himalayan Region comprises the whole of the Tibetan plateau, inner and outer, together with the river gorge country, Chinese Tibet, and the Great Himalaya. The Flora is a mountain flora similar in appearance to that of the European Alps. It includes Himalayan, Indo-Malayan, and Chinese (Eastern Asiatic) species, together with many endemic genera.

MAP 1.



to cut deep grooves for themselves through the lofty containing walls, in order to make their escape to the plains below.

The climate is much moister than that of the plateau and far less harsh ; but necessarily it varies greatly with the changes of altitude ; the flora is very rich, and much of the river gorge country is covered with forest. Two physiographical types can be recognized : the upper gorge country, inside the main containing wall of the plateau, with a comparatively dry climate and an alpine flora, and the lower gorge country, clothed with dense forest. This last division, though it includes the Tibetan districts of Zayul and Pemako, and is politically part of Tibet, is not geographically part of Tibet, lying outside the great ring of mountains which contains the main plateau. Further east, beyond the Yangtze, is a fourth division usually called Chinese Tibet. This is really an outlying part of the river gorge country, with a still softer climate and an equally rich flora. It is not under the Lhasa government, and is excluded from this review.

With this introduction to the physiography of Tibet, I shall now state the main problem.

East of Sikkim the Great Himalayan range trends in an east-north-east direction, till it culminates in the high peak Namcha Barwa, 25,500 feet, which rises like a steeple above the gorge of the Tsangpo.

Does the Great Himalayan range end here, abruptly truncated, in this stupendous bluff overlooking the plain of Assam ; or does it extend across the Tsangpo gorge continuing in the same general direction towards China ? \*

Now this is partly a geological problem, because it is partly a question of the underlying framework of the mountains, of the age of the rocks, and of their relations to one another. Unfortunately, the geology of this region is practically unknown, and it will need many years of work by competent geologists to unravel it.

Meanwhile, it is a geographical problem in the widest sense. Let us see what light we can throw on it, by looking at the country as seen by a traveller passing through it.

On any small scale physical map of S.E. Asia, we notice a feature unique in the geography of the globe. Those rivers which rise on the edge of the great plateau and flow eastwards or south-eastwards across the outer plateau, here change their direction to the south, gradually or abruptly. There is nothing especially remarkable in that. But, strangely enough, although their sources are hundreds of miles apart, they all break through the containing wall of the plateau close together. Thus they converge, and for two hundred miles flow parallel to one another, separated by high ridges, within a narrow strip of country. After escaping through the containing wall they again diverge widely.

\* Or does it turn abruptly south-westwards, follow the coast of Burma, and continue eastwards through Java as the Malay arc ?

This feature is remarkable enough. But the compilers of maps have made it more remarkable than ever Nature made it, by emphasizing the ridges between the rivers, turning them into great meridional ranges, bending them round to the north-west, parallel to the rivers and truncating the Great Himalayan range.

This is an unjustifiable proceeding; because, although that is how the country appears to the traveller, who can only see a very small part of it at any one time, the interpretation of what he sees may be quite different. If he makes many journeys as I have done, he will probably arrive at a different conclusion.

The Great Himalayan range extends along the southern frontier of Tibet for hundreds of miles, rising directly from the plains and forming a continuous barrier. Plains and plateaux here approach one another closer than anywhere else, and over the Himalayan range is still the easiest way into Tibet from the south. East of the Tsangpo bend, however, there appears to be a breach in the containing wall of the plateau, through which all the big rivers find their way out to the plains; and through this breach entry into Tibet might surely be gained without the arduous labour of climbing over the barrier. The traveller ought to be marching parallel to the great ranges—at least, according to the map. Nothing could be further from the truth, for, although it is possible to pass through the river gorges and to reach the plateau behind, such a journey is long and troublesome. It involves traversing almost impassable gorges.

Two rivers, however, the western branch of the Lohit and the eastern branch of the Irrawaddy, rise further south. They have cut only minor gorges, and flow in comparatively wide valleys, so that it is easy to follow them to their sources. Having done so, one still finds oneself at the foot of a great snowy range, which must be crossed before the outer plateau of Tibet is reached.

South of this snowy range the country has been cut up by rivers into a tangle of mountains, which form an outlying defence system difficult to penetrate. This is the lower gorge country, not properly a part of Tibet at all, since it never formed part of the plateau. When this snowy range has been crossed, the traveller finds himself in the upper gorge country and on the threshold of the outer plateau. This river-gorge country, then, like the Great Himalayan range further west, forms a high rain-screen between Burma-Assam and the Tibetan plateau. In the interpretation of this country, its structure and history, lies the clue to the distribution of plants and animals throughout south-eastern Asia.

Now the argument in favour of meridional mountain ranges east of the Tsangpo is at least logical. The Himalayan earth movement is, as already remarked, a recent movement of Eocene-Miocene age. In the Burma-Yunnan area there is a meridional uplift which is infinitely older than the Himalayan uplift—post-Carboniferous, but pre-Triassic, according to Gregory,—belonging



to an entirely different system of mountain building. We need only extend this Burma arc, as it is called, northwards and westwards, in order to make it cut right across any possible eastward extension of the Himalayan axis—as the map makers, in fact, do. But there is no proof whatsoever that this Indo-Malayan uplift extends northwards, much farther than the 28th parallel, particularly west of the Salween, though it may do so. Nor are any high peaks of this age known. Indeed, as Gregory showed, the rocks have been worn down to a peneplain, and that long before the Himalayan movements began. So that the existence of this Burma arc in no way challenges an eastern extension of the Great Himalayan range. Gregory himself believed in its extension and found evidence that the Himalayan movement had affected pre-Eocene rocks in Yunnan\*. The Himalayan earth movements, acting from the north at right angles to the much older unyielding platform of Yunnan, may have caused a rending and shearing of the rocks sufficient to start lines of weakness of which the rivers were later to take advantage.

The problem now is, what direction does this Himalayan extension follow? This is mainly a physiographical problem. The topographical evidence is by no means complete, the region being mostly unexplored. But there is no evidence against a continuation of the Himalayan range beyond Namcha Barwa. The apparent meridional ranges between the Tsangpo and the Yangtze are not necessarily meridional ranges at all. If the highest areas are plotted on the map, they are found to extend along an east-south-east to west-north-west alignment in a comparatively narrow belt, *parallel to the strike of the rocks*. This belt forms the southern edge of the plateau, and it has been cut through by parallel rivers at right angles to the strike, isolating strips of the old east-west uplift and leaving them standing out as meridional ranges. The highest peaks on each meridional range rise far above the general level, to north and south, but are comparable with each other. Many years ago, the celebrated naturalist Brian Hodgson suggested that the high Himalayan peaks stood at the ends of spurs jutting out from the Tibetan plateau, and not on a continuous range. To-day the continuity of the Great Himalayan range west of the Tsangpo bend is not questioned, and the theory of isolated meridional spurs is discredited. Similarly these meridional ranges between the Yangtze and the Tsangpo are no more than greater spurs projecting from the Himalayan extension; and the discovery in 1933 of a great snow range at the source of the Zayul River makes it clear that this *is* the Himalayan extension.

If one travels northwards through the river gap—that is to say anywhere between the Tsangpo and the Yangtze, one must either cross a great snow range or, following one of the big rivers, pass *through* a great range in a profound gorge, before reaching drier country.

Last year I found and crossed a great snow range in latitude 29° N. at the source of the western branch of the Zayul River. Reaching Shugden Gumpa,

\* 'Philosophical Transactions of the Royal Society of London', Series B, vol. 213. Also 'Geographical Journal', March 1923.

at the source of the Nagong river, I continued northwards, crossed another pass, and descended to the Salween. Later I traced the snow range in a north-westerly direction for about 50 miles; the gap between this point and Namcha Barwa is 80 miles. Though the peaks on this range are probably not so high as Namcha Barwa, several of them are in the neighbourhood of 22,000 feet.

Although in my journey to the Salween I crossed another high pass over a great range of mountains, with many snow peaks and small glaciers, the alignment of this range is also roughly N.W.-S.E., and there can be no doubt that it is all part of the one great range—the Tsangpo-Salween divide. It appears to be two ranges only because the Nagong River, flowing N.W. along the strike, and the eastern branch of the Zayul River, flowing S.E. along the strike have cut grooves along the wide crest of the range. The total breadth of the Tsangpo-Salween divide here is not more than 60 miles, which is much less than the breadth of the Great Himalayan range. Sir Sidney Burrard in 1907 favoured the view that the Ninchinthangla range of Tibet—the Tsangpo-Salween divide—curves round to the south and becomes the Irrawaddy-Salween divide. If that were so, the Himalayan range must end at the Tsangpo. In the latest edition of his great work \*, however, he has abandoned that view.

The core of the range (Tsangpo-Salween divide) is composed of granite and gneiss, with schists exposed in the valleys to the south. But north of the Ata Kang pass I crossed bands of slate and limestone; and still further north, on the descent to the Salween gorge, belts of hard greyish siliceous limestone, red sandstone and conglomerate, black slate, and brown shale stretch across the country. The strike of these rocks is invariably between N.N.W.-S.S.E. and W.N.W.-E.S.E., the strata having been thrown into great folds by pressure acting from the north or north-west. The alignment for the Himalayan extension here put forward agrees in part with that suggested by J. W. Gregory ('The geology and physical geography of Chinese Tibet', *Phil. Trans. Roy. Soc. series B*, vol. 213). These rocks, then, have been affected by the Himalayan fold movements. The strike of the siliceous limestones observed by Murray Stuart north-east of Fort Hertz, in the Nam Tamai valley, which I subsequently traced across the Irrawaddy-Tsangpo divide, is also N.W.-S.E. approximately parallel to, and perhaps continuous with, the Shugden Gumpa limestone †.

If the alignment of the snow peaks discovered in 1933 is continued towards the east, it will pass through a group of peaks over 19,000 feet high on the Irrawaddy-Tsangpo divide. These peaks are only 60 miles distant. Continuing the alignment, the following nuclei of high peaks occur in order from north-west to south-east: on the Salween-Irrawaddy and Salween-Mekong divides, about 50 miles distant; on the Mekong-Yangtze divide, 25 miles distant; and east of the Yangtze, 50 miles distant. Wider gaps than these

\* 'A sketch of the geography and geology of the Himalaya Mountains and Tibet', by Colonel S. G. Burrard and H. H. Hayden. (Second edition, revised by S. G. Burrard and A. M. Heron.)

† 'Records of the Geological Survey of India', vol. 1, 1919.

occur between the high peaks on the Great Himalayan range; and it has to be remembered that the river gorge country has been tremendously denuded. Further evidence for the extension of the Himalayan range eastward towards China along this alignment may be summarized as follows :—

(1) The presence of a great gorge on the Salween River, between 28° N. and 29° N. accompanied by an abrupt change from moist subtropical to arid conditions, exactly as in the Tsangpo gorge. The Yangtze also breaks through an impassable gorge in the required latitude. Very high peaks occur on either flank of the Salween gorge. I explored this Salween gorge in 1911 and 1913–14. In 1921–22 I observed the Yangtze gorge.

(2) The steady southward slope of the country from this alignment and the absence of any outstanding peaks to the south.

(3) The comparative levelness of the plateau north of the alignment, again without any outstanding peaks, until the next E.-W. fold range north of the Salween is reached.

(4) The steady increase in altitude of the peaks as the river gap is left behind and the drier country of western China approached. This is mainly a climatic effect, consequent upon the wide breaching of the ranges.

(5) The preponderance of an east and west relationship in the flora over a north and south relationship, in spite of the tremendous advantage the latter obtained in recent geological time. For, while the east and west continuity was interrupted by the presence of an ice-cap, the Tibetan flora was being driven southwards by that same advance of the ice. Yet when the ice at last retreated, the irruption of the flora into the southern mountains had made only a slight impression; while the continuity of flora, east and west, especially across the river gap, although impaired, was still obvious\*.

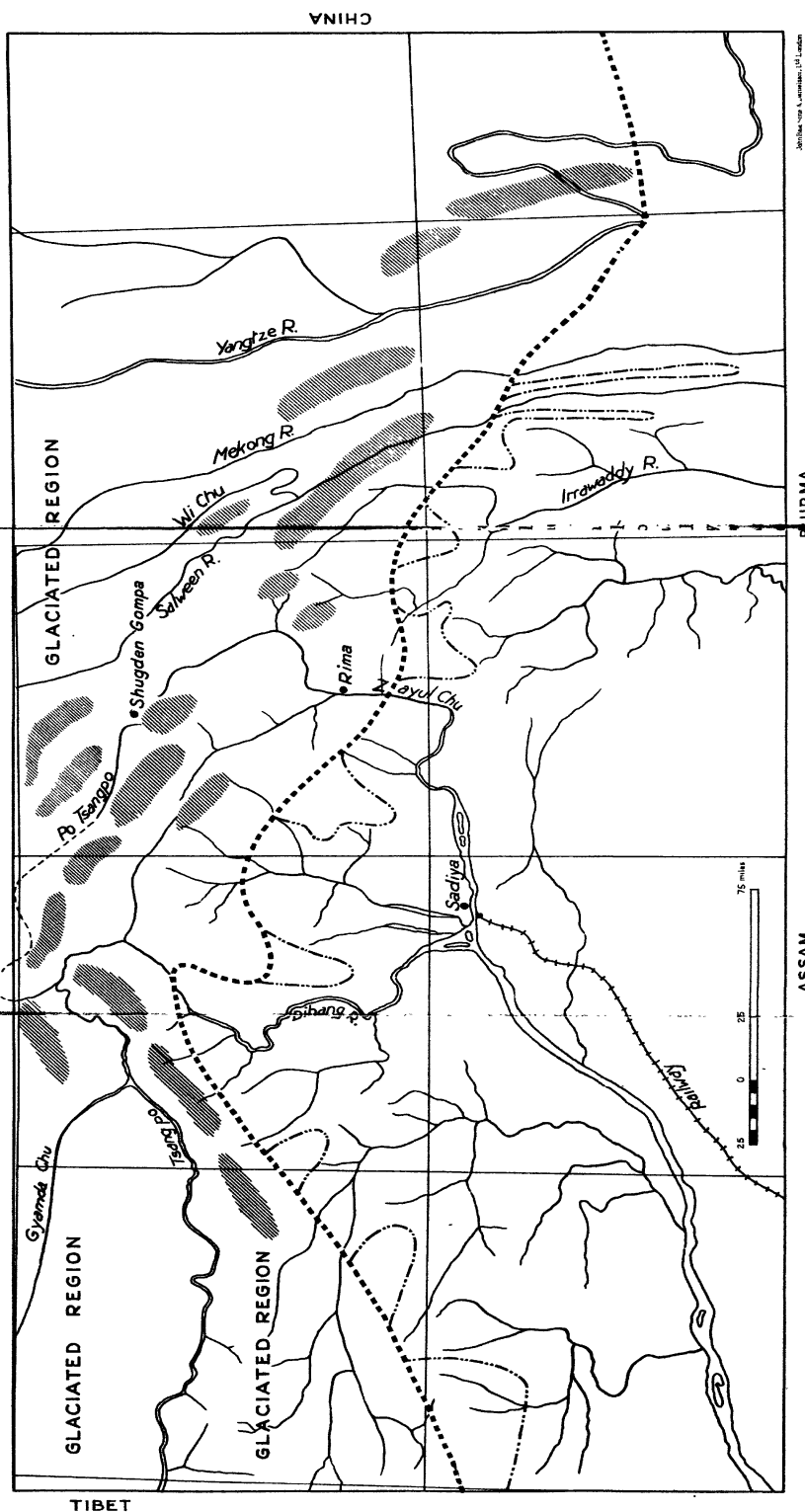
(6) The distribution of certain groups of plants, e.g. *Magnolias*, *Nomocharis*, certain *Primulas* and *Rhododendrons*, follows this line very closely. Some

\* The following plants, previously known only from the eastern Himalaya, have lately been discovered on the Assam or Burma frontier ranges, east of the Tsangpo :—*Bryocarpum himalayense*, *Lindenbergia Hookeri*, *Sabia parviflora*, *Acer sikkimense*, *A. Campbellii*, *Meconopsis paniculata*, *Aucuba himalayica*, *Ilex Hookeri*, *I. intricata*, *I. odorata*, *Primula Wattii*, *P. muscoides*, *P. prenantha*, *Loxostemon pulchellus*, *Rosa Moyesii*, *Viola Hookeri*, *V. Thomsoni*, *Lycocateria stipulata*, *Lychnis nigrescens*, *Buddleia Hookeri*, *Pedicularis gracilis*, *P. Pantlingii*, *P. gibbera*, *P. Gamnieana*, *Rhododendron Griffithii*, *R. Nuttallii*, *R. lanatum*, *R. pumilum*, *R. vaccinioides*, *Paraquilegia microphylla*.

The following plants, previously known only from western China, have lately been found on the eastern Himalaya, west of the Tsangpo bend :—*Primula szechuanica*, *P. chungensis*, *Meconopsis betonicifolia*, *Viola Delavayi*, *Ilex Pernyi*, *Lonicera setifera*, *Euonymus taliensis*, *Arenaria Delavayi*, *Rhododendron repens*, *R. sino-grande*, *R. arizelum*, *Adonis brevistyla*.

A large number of plants, particularly alpine, had long been known to be common to western China and the Himalaya. Amongst them :—*Draba alpina*, *Myosotis Hookeri*, *Roscoea alpina*, *Iris kumaonensis*, *Clematis montana*, *C. urophylla*, *Pegaeophyton scapiflorum*, *Didissandra lanuginosa*, *Bergenia purpurascens*, *Morina betonicoides*, *Diplarche multiflora*, *Rosa sericea*, *Potentilla fruticosa*, *Diapensia himalaica*, *Magnolia Campbellii*, *M. globosa*, *Paraquilegia microphylla*, *Eriophyton Wallichianum*.





MAP II. THE ICE FRONT IN THE RIVER GORGE COUNTRY



groups or species keep to the north of it, others to the south of it. Thus the range has been both an embankment along which plants have spread and a barrier between a drier alpine climate to the north and a moister forest climate to the south.

(7) The insects, particularly those from the forested southern flank of the range, are entirely Eastern Palearctic, and not, as one might have expected, Oriental. The affinities of the butterflies are with western China, of the Diptera with Tibet and western China, of the Orthoptera with western China.

(8) If the flora of one of the apparent meridional ranges is examined, it is found to differ more to north and south of its dominating snow peak than it differs from the flora of the meridional ranges which lie on either side of it. This is merely a special application of the general principle that the flora follows east and west rather than north and south lines; but it is a significant one.

I will now outline the course of events in S.E. Asia, so far as they can be ascertained. The first revolutionary change took place when what was formerly the sea bottom was upraised until it became the greatest mountain range and the highest plateau in the world. The second revolutionary change took place much more recently, when arctic conditions came on and grew in severity until a vast ice-cap was formed covering the entire river gorge country. A belt of ice extended right across the eastern Himalaya, the river gorge country, and western China, completely cutting off the three great southern peninsulas \* from the heart of Asia. The southern limit of this ice-belt, so far as I have been able to trace it across the river gap, is shown in Map 2; but a few large glaciers probably advanced even further south.

Every traveller in these regions has observed the retreating glaciers and remarked on their former extension. There is, I think, overwhelming evidence, not merely for the former extension of glaciers, which is obvious enough, but for a glaciation so intense that an entire ice-belt extended along the marginal ranges of the plateau.

Another proof of the plateau nature of the lower gorge country is afforded by the remarkably uniform heights of the peaks between the deep river valleys. This is especially noticeable at the headwaters of the Irrawaddy. I was very much struck by the views of the long level spurs which flare southwards from the Lohit-Irrawaddy divide, as seen from the upper Seingku valley in 1926 and from the Adung valley in 1931. Reference to the map where the country has been rigorously surveyed confirms this impression. There are literally hundreds of peaks over an area of 20,000 square miles at the sources of the Irrawaddy between 15,000 and 18,000 feet high. The only peaks higher than this, and they are few, lie on the N.W.-S.E. belt. The same may also be said of the Lohit and Dihang valleys on the Assam frontier. Throughout this area signs of glaciation are unmistakable. Snow-beds still exist in large

\* i.e. India, the Malay Peninsula, and Indo-China.

numbers—the last remnants of once extensive glaciers. The upper valleys all show the 'tread and riser' structure associated with retreating glaciers. The ice-shelf\* is a universal feature. Small glacier-lakes abound. Naturally the moraines have been washed away; there are ice transported boulders in the Seinghku valley.

I have examined all the great river valleys from the Tsangpo to the Yangtze for traces of glacier action, and have explored most of them for many miles in the critical regions. The southern limits of the ice can therefore be set down with some degree of assurance. On the Tsangpo it reached at least to  $29^{\circ} 30'$ , in the Dibang valley to about  $29^{\circ}$ , in the Lohit valley to  $28^{\circ} 15'$  (south of Rima), in the Irrawaddy valley (Nam Tamai headwaters) to  $28^{\circ} 15''$ , in the Salween and Mekong valleys to  $28^{\circ}$ , and in the Yangtze valley to  $27^{\circ}$ . The steady advance of the ice as one travels eastwards is significant; it corresponds closely with the alignment of the Himalayan extension—that is to say, with the source from which the glaciers must have been derived.

Between these two great revolutions, the uplift of the Himalayan ranges and their glaciation, occurred others of less importance.

According to Gregory, during Pleiocene time the drainage lines of the Tibetan rivers were formed by meridional fracture, at the same time that great basins were being formed by subsidence. After that came an arid period, during which thick deposits were laid down in the basins and valleys.

The present distribution of plant and animal life in S.E. Asia is mainly a post-glacial distribution, and in order to understand it we must first follow the sequence of events during the Quaternary period. We need not concern ourselves with the flora of S.E. Asia—at least the mountain flora—previous to the glacial epoch, since it must have been completely exterminated. If any fragments escaped, and there is no evidence that they did, they were driven south. But after the retreat of the ice the flora flowed northwards again.

Recent botanical exploration has shown that the affinity of the eastern Himalayan flora lies almost entirely with western China across the gorge country. It does not lie with the southern ranges, except in a minor degree†, although the mountain ranges appear to be continuous in this direction. Both alpine flora and temperate forest extend east and west in continuous belts.

The fact that three distinct floras meet without mixing in S.E. Asia is explained by the separation of these areas by continuous ice-belts and desert areas. Before the glacial epoch the flora was no doubt more uniform. But long isolation, under different conditions, allowed distinct floras to develop in China and Indo-Malaya. As the ice continued to retreat the flora gradually flowed into central Tibet, which was still completely isolated from the sea. Meanwhile, a fourth and infinitely richer flora was reforming on the great

\* When a shallow U-shaped glacier valley ploughed in the plateau has a deep nick cut in its floor by a river, a ledge is left on either side just beneath the sierra marking the original height of the plateau. This ledge I call the ice-shelf. See 'Geographical Journal', May 1930.

† This might be to some extent due to increase of temperature southwards.



mountain ranges with Chinese, Himalayan, and Indo-Malayan affinities. An endemic element now made its appearance, and many new genera emerged, e.g. *Nomocharis*, *Cremanthodium*, *Omphalogramma*, *Bryocarpum*. Gradually this Sino-Himalayan flora spread east and west from the river gorge country and penetrated far into Tibet.

Certain groups of species kept entirely south of, or north of, the rain screen, even where the country is much broken—'Candelabra' Primulas, for example, and several groups of Rhododendrons.

Finally, I will add a few words about the glaciers of the river gorge country as they appear to-day. Glaciers abound in all the mountain ranges above the big rivers from the Tsangpo to the Salween. They are mostly hanging glaciers, especially north of Shugden Gumpa. On the great snow range I found one glacier to be about 10 miles long, and two others not much inferior to it. All are retreating. All once reached down to larger valleys, which were formerly wide shallow valleys on the ancient plateau, themselves filled with ice. Eventually as the ice retreated, the grit laden rivers cut deep gorges for themselves in the floors of the valleys.

These glaciers all originated in an ice sheet which extended east and west between the meridians of  $94^{\circ}$  and  $100^{\circ}$  and the parallels of  $28^{\circ}$  and  $32^{\circ}$ , so far as the river gorge country is concerned. The whole of this region was originally a high glaciated plateau, across which the mountain ranges trended east and west. North of the 30th parallel the plateau extends for a vast distance; but it seems probable that the ice-belt was not so extensive as the plateau, the interior of Tibet being too dry, even then, to support great glaciers. On the other hand, the ice-belt probably extended far to the east and west, into China and down the southern slope of the Himalaya.

Two extensions of the flora are possible. The first is a distribution north and south across the edge of the plateau, following the older mountain system of Burma-Yunnan. That is the most natural direction. The second is an east and west distribution along the edge of the Tibetan plateau into China.

The north to south distribution, such as it is, follows the line of the Malay Peninsula, reappearing in the islands of the archipelago. Thus it follows the Malay arc. The relationship is remote, yet it exists. According to this view the islands must have become separated from the mainland—and from each other—quite early during the last glacial epoch. Only thus can we account for the lack of similarity in the island floras; but also only thus could Java have got its Rhododendrons, and its solitary Primula\*. The east-west

\* *P. imperialis*, hardly distinguishable from *P. prolifera*. A. R. Wallace notes that Java must have been separated from the mainland not earlier than late Pliocene times. His arguments all tend to prove a recent separation, and caution alone persuades him to put it as early as Pliocene time (The Malay Archipelago). I am inclined to put the final separation of Java much later. It is inconceivable that the Javanese Rhododendrons reached the islands after their separation from the mainland. But it is just possible, though highly unlikely, that they arrived there during Pliocene times, before the first separation of Java. For, unless the Malayan mountains were then higher, what caused them to travel so far south? The great ice push is the only known agency.

distribution is much more obvious. More and more have Sikkim and eastern Himalaya plants generally been discovered to the east of the Tsangpo gorge ; while plants previously thought to be peculiar to western China have continually turned up west of the Tsangpo gorge. Going still further east, we can trace the connection right across to Formosa on the one hand, to Japan on the other, in spite of the breach in the wall caused by the rivers.

The Chang Tang is all that remains of the original plateau. The outer plateau is the first stage in its reduction. The river gorge country is the next stage.

If the strip of river gorge country was really raised to 16,000 or 18,000 feet during the late Primary epoch, it could not have been uplifted as a series of parallel ranges, because the river gorges did not exist. It must therefore have been upraised as a plateau. But an immense amount of denudation has taken place since those remote times. The Hercynian uplifts have been worn down to their roots, forming first a plateau and ultimately a peneplain. Then came the Himalayan movement to galvanize it into life and give it a new form. The ancient peneplain probably affected the direction of the movement, but the movement also affected it. After that it was covered by an ice-cap and furrowed by glaciers. A further uplift of the Himalaya in recent times may have increased the gradient of the river beds and encouraged the cutting of the gorges after the retreat of the glaciers. I conclude that the present north-south grain of the country is not only a post-Himalayan feature, but entirely post-glacial. The mere fact of an ancient Hercynian uplift along the Burma-Yunnan frontier has nothing to do with the present north to south grain, except in so far as it diverted and blanketed the later alpine movements.

The drainage of Tibet, consequent upon the first Himalayan movements, was east and west, as seen in the upper courses of the Indus, Sutkaj, Yangtze, Salween, Tsangpo, and Yellow Rivers. There is no evidence as to whether the rivers in these troughs flowed east or west. Probably they were short streams, flowing into salt lakes on the great plateau. There may have been chains of lakes. Subsequently south-flowing rivers cut back through the main range by head erosion and captured troughs on the plateau. The opening (river gap) in the Himalayan range let in the monsoon. The lower courses of the rivers received more water and scoured their channels more rapidly, thus increasing the gradient, which was further increased by uplift at the head and by the melting of the glaciers. The present rivers are all combined rivers, and one (the Dihang-Tsangpo) may be reversed—that is, it may formerly have flowed from east to west \*.

The cutting of the gorges could not have begun until after, possibly not till long after, the maximum advance of the ice. We might put it at not less than 25,000 nor more than 50,000 years ago. If we allow 50,000 we are faced with the fact that the Himalaya and the plateau were practically naked at that

\* Burrard : 'A sketch of the geography and geology of the Himalaya Mountains and Tibet' (1st edition).

time. The flora was returning timidly from the south. On the great Himalayan range it had not been driven very far, nor did it cross the plains—there is no sign of it south of the Ganges valley, although Ceylon received one *Rhododendron*. South of the river gorge country, however, the flora could travel freely to Malaya and the Indies. Then came the return, and having returned it spread out east and west before the river gorges were cut.

If the gorges were filled up to a depth of 10,000 or 12,000 feet, the arrangement of the present snow-peaks will clearly be seen to extend along a more or less east-west alignment, not north and south. If the rivers had deepened their beds by 3 in. a year, on the average, they would, in 50,000 years, excavate them to a depth of 12,500 feet. That does not seem very improbable.

Moreover, between the groups of snow-peaks, on any one river divide, are much lower areas—depressions, one might almost call them. The snow-peaks to east and west of Kakarpo, for instance, are much closer to it than the next peak to the north—Damyon. Similarly Orpo to the north-west and Kenichunpu to the west are nearer than the next snow-peak south of Kakarpo on the same range. The inference is that these gaps represent the remains of east and west troughs on the ancient plateau before the gorges were formed.

To-day one may marvel how the flora remains so uniform across these deep river gorges and apparent ranges of mountains, and why it changes so rapidly as one travels southwards along the ridges and river corridors, in spite of the fact that it invaded the south and left its mark so far afield as Java and New Guinea. And one may marvel also why it is that as one goes northwards, up one river gorge, the climate changes quite abruptly within a few miles, though it does not do so as one goes eastwards across a dozen river gorges and a dozen snow-ridges.

The reason is simply that the east-west rain screen, the Alpine-Himalayan uplift is still there; though it has been broken into blocks and obscured by secondary meridional ranges due to river action. The climate changes here exactly as it changes when one crosses the Great Himalayan range further west. The flora is uniform from Namcha Barwa eastwards to the Yangtze, exactly as it is uniform from Namcha-Barwa to Nepal, in parallel belts north and south of the rain screen.

### III. THE CHANG TANG.

The Chang Tang is the great plateau proper, and represents the popular idea of Tibet at the beginning of the present century. Briefly, it is a vast undulating saucer with an average elevation of about 16,000 feet. The drainage is internal, hence the numerous lakes, fed by short rivers flowing down from the edge of the saucer, are salt or brackish. Some of these lakes are large, but all of them were formerly much larger. Parallel ranges of mountains, rising only a little above the general level of the plateau, diverge from the Pamirs and trend eastwards; they are separated by wide shallow troughs.

Northwards the Chang Tang is bounded by the Kun Lun which separates

it from the central Asian depression, southwards by the Trans-Himalayan range which separates it from the Tsangpo valley. These ranges support the Chang Tang between them.

Eastwards the Chang Tang passes insensibly into the outer plateau, where the headwaters of several big rivers rise and flow outwards. The watershed is very flat ; but this region is unmapped, so that it is not possible to indicate the limits of the Chang Tang and of the outer plateau exactly. Strictly speaking, the eastern boundary of the Chang Tang is where the Salween, Mekong, and Yangtze and their affluents rise and the water begins to flow away eastwards and southwards. But for some distance eastwards from the ultimate sources of these rivers there is scarcely any change in the general features of the plateau or in the vegetation.

It was the Chang Tang which nearly all the Tibetan travellers of the 'nineties of last century and the first decade of the present century explored. So long as Tibet was completely closed to outsiders, it was possible to explore only the uninhabited regions ; travellers who penetrated into inhabited country were stopped, sooner or later. Bower, Wellby, Sven Hedin, and Littledale all crossed the Chang Tang ; Deasy, Rawling, and others explored parts of it. From their writings we can form some idea of that terrific land.

The winters are extremely severe. Even in summer the temperature scarcely rises above freezing-point.

More inimical to vegetation than the cold, however, is the dryness of the atmosphere, intensified by the fierce winds which perpetually sweep the plateau. There is much salt in the soil. Sparse as the vegetation of the Chang Tang is, it is more varied than might be expected from what has been said. It comprises some grasses and annual herbs, with perhaps a few cushion plants ; the affinity of the flora is almost entirely with the Himalaya.

The Chang Tang is uninhabited, and the greater part of it must be regarded as, physiologically, a desert. Yet despite the scanty vegetation, great herds of *kyang* and antelope roam over it. Further east, on parts of the outer plateau which are scarcely distinguishable from the Chang, yak abound.

The area of the Chang Tang is about 350,000 square miles, and the snow-line stands at 18,000-19,000 feet. No systematic botanical collecting has been done in this region, but most travellers have collected such plants as they came across, and it is quite probable that every species is known. I am indebted chiefly to the works of the explorers mentioned by Hemsley for the list of plants, comprising about 50 species, found on the Chang Tang. Most of western Tibet, including Ladak and Baltistan ('Little Tibet'), though geographically part of the outer plateau, has a climate scarcely less severe than that of the Chang Tang ; and the same may be said of the Trans-Himalayan range north and west of Lhasa. The altitude, too, of Little Tibet averages 16,000 feet. It is therefore not surprising that the flora of these regions, though richer in species than the Chang flora, should be similar. Tsaidam, though several thousand feet lower than the Chang Tang, is also part of the

closed drainage-area. It is encircled on the north by the Altyn Tagh, a range which branches off from the Kun Lun, and it drains into the Tarim basin. Its flora is very similar to that of the Chang Tang. The Chang flora is so scanty that it will be convenient to give it here in full.

*Flora of the Chang Tang.*

- Ranunculus tricuspidis* Maxim.  
 — *pulchellus* C. A. Meyer (C.).  
*Capsella Thomsoni* Hook. f. (C.).  
*Cheiranthus himalayensis* Camb.  
*Alyssum canescens* DC.  
*Draba alpina* Linn.  
*Sisymbrium humile* C. A. Meyer (C.).  
*Pegaeophyton scapiflorum* (Hook. f. et Thomas) Marquand et Shaw  
*Myricaria prostrata* Hook. f. et Thomas  
*Thylacospermum rupifragum* Schrenk  
*Astragalus Malcolmii* Hemsl. et H. H. W. Pearson  
 — *Arnoldii* Hemsl. et H. H. W. Pearson  
*Thermopsis inflata* Cambess.  
*Chamaerhodos sabulosa* Bunge  
*Sedum Rhodiola* DC.  
 — *tibeticum* Hook. f. et Thomas  
*Selinum striatum* Benth.  
*Peucedanum Malcolmii* Hemsl. et H. H. W. Pearson  
*Tanacetum tibeticum* Hook. f. et Thomas  
*Artemisia Wellbyi* Hemsl. et H. H. W. Pearson  
*Cremanthodium nanum* (Decne.) W. W. Sm.  
 — *plantagineum* Maxim. forma *goringense* (Hemsl.) R. Good  
*Crepis flexuosa* Clarke  
*Taraxacum bicolor* DC.  
*Saussurea tridactyla* Sch.-Bip. ex Hook. f.  
 — *Wellbyi* Hemsl.  
*Pleurogyne brachyanthera* Clarke  
*Microula tibetica* Benth.  
*Pedicularis cheilanthifolia* Schrenk  
*Nepeta longibracteata* Benth.  
*Eurotia ceratoides* C. A. Meyer (C.).  
*Polygonum aviculare* Linn.  
 — *Deasyi* Rendle  
*Rheum spiciforme* Royle  
*Euphorbia tibetica* Boiss.  
*Urtica hypoborea* Jacquem.  
*Ephedra Gerardiana* Wall.  
 — *distachya* Linn.,

*Allium senescens* Linn.  
 — *Semenovi* Regel  
*Juncus Thomsoni* Buchenau (C.).  
*Triglochin palustre* Linn. (C.).  
*Carex Moorcroftii* Falconer  
*Stipa sabulosa* Turcz.  
 — *stenophylla* Wahlenb.  
*Stipa purpurea* Griseb. (C.).  
*Avena subspicata* Claviv. (C.).  
*Agropyron Thoroldianum* Oliver  
*Poa alpina* Linn. (C.).  
*Festuca valesiaca* Schleich. (C.).  
*Glyceria distans* Wahlenb. (C.).  
*Elymus junceus* Fisch.  
 — *lanuginosus* Trin. ex Ledeb.

NOTE.—A (C.) after a species denotes its occurrence in the true Central Asian region, comprising Turkestan and Mongolia.

The above fifty-three species of flowering plants are all that appear to be known from the Chang Tang. Of these, eleven (including five grasses), widely distributed in the North Temperate zone, are probably recorded also from the Central Asian region north of Tibet. Hemsley, in his distribution table of the Tibetan flora, records 23 of the above species as 'Mongolian', i.e. Central Asian. From the altitudes given, however, and from an examination of maps, whence the recorded localities can be found from the explorer's narratives, it is clear that nearly all these plants were collected in Tibet and not in Turkestan.

Of the 53 Chang species, 38 are known also from the outer plateau, and 5 of these extend to the river gorge country. Of the remaining 15 species, known from no other part of Tibet but the Chang, only 10 are endemic, the remainder being more or less widely distributed. There are no genera peculiar to the Chang Tang.

Thus there is no reason for separating the Chang Tang from the rest of the plateau on botanical grounds. It is a matter of geographical convenience only. The Chang flora is much poorer in species and has no woody plants\*, but it is only a difference of degree. Further exploration of the outer plateau will probably reduce the number of endemics on the Chang.

#### IV. THE OUTER PLATEAU.

The outer plateau, which includes the provinces of Ü and Tsang (called Ü-Tsang) is to-day perhaps the best-known part of Tibet, because the cities of Lhasa, Shigatse, and Gyantse belong to it. Little Tibet also, and the Manasorawa region at the sources of the Indus and Sutlej; the country round the headwaters of the Mekong, Salween, and Yantze Rivers; and the Koko Nor region, all belong to the outer plateau. The physical features are those

\* *Myricaria*, *Ephedra*, and *Tanacetum* excepted,

of the Chang, except that the drainage is external and the mountain ranges more clearly defined. There are fewer lakes, and those fresh water. The higher regions of the outer plateau are, as already remarked, as lofty as the Chang Tang itself, and, having a similar climate, possess a similar flora; but the outer plateau includes also great residential areas, much lower in altitude, with a milder climate.

The trade route between India and Lhasa is, beyond Phari, entirely confined to the outer plateau. In the south the Tsangpo valley extends across it from west to east for 500 miles. In the north the Salween, Mekong, and Yangtze drain the country between the Chang Tang and the river gorge country. Between the Great Himalayan range in the south and the Chang Tang in the north several ranges of mountains traverse the outer plateau. South of the Tsangpo is the Ladak range; north of the Tsangpo is what was formerly called the Kailas Range, now included in Sven Hedin's Trans-Himalaya \*. There are probably other ranges.

The average altitude of the outer plateau may be taken as 16,000 feet in Little Tibet and everywhere on the fringes of the Chang Tang, and as 12,000 to 14,000 feet in residential areas, such as the Tsangpo valley.

The climate is continental, but not Arctic as on the Chang Tang—except on the fringes. Wind, as everywhere in Tibet, is the great enemy of plant life; the dryness of the atmosphere and the dryness and coldness of the soil for long periods combining to produce semi-desert conditions.

South of the Tsangpo the plateau reaches the frontier of India along the northern slopes of the Great Himalayan range; consequently the flora of this region is well known to Indian botanists, especially along the trade routes. Since the British Mission to Lhasa in 1903-4, several botanists have collected round Phari and Gyantse, notably Sir William Wright Smith, Mr. Cave, and Mr. F. Ludlow. The earlier collections of Hooker round the Donkia La and of members of Sir Francis Younghusband's mission on the trade route are well known. Western Tibet, too, has been well explored, and in recent years the botanical collections of Professor S. R. Kashyap have added to our knowledge of the more inhospitable parts of the outer plateau.

Sven Hedin is the only traveller who has explored Trans-Himalaya, and for our knowledge of the upper courses of the Tibetan rivers we are mainly indebted to Russian and French explorers—Przvalsky, Kolsov, Bonvalot, Prince Henry of Orleans, Dutreil de Rhins, and to W. W. Rockhill. The English explorers of last century, however (Bower, Wellby, and others), all marched from the Chang Tang into China via the headwaters of the Tibetan rivers—and all of them collected herbarium specimens.

The residential regions to the south-east between Lhasa and the river gorge country, though the richest part of the outer plateau, have been less explored botanically—and there is little except my own explorations of 1924 to go on.

\* I have throughout adhered to the nomenclature adopted by Sir Sidney Burrard and the Survey of India.

In general, the outer plateau is bare of forest, and trees are confined to the water courses and to cultivated valleys, where they are protected. When woody vegetation first appears it is usually Juniper scrub. Species of Willow, *Ulmus pumila*, Poplar, *Hippophaë*, and a few other trees occur sparingly; but gradually even these die out, and westwards and northwards the country resembles more and more closely the Chang Tang.

In the Tsangpo valley, east of Lhasa, there is much blown sand, and a scrub flora, including *Berberis*, *Sophora Moorcroftiana*, *Buddleia*, *Caragana*, and *Potentilla fruticosa*, becomes prominent. The first big tree to appear by the river is a species of Juniper. Further east, at the head of the gorge country, forest begins. Thus eastwards and southwards the semi-desert and alpine flora of the outer plateau is replaced by the forest flora of the river gorge country, though many characteristic alpine plants are repeated on the high rocky sierras which traverse the gorge country, as well as on the Great Himalayan range itself.

Thus, though there is very little woody vegetation on the outer plateau, there is a fairly rich high alpine flora.

In general, one may say that the flora of the outer plateau in the north-west resembles that of the Chang Tang, in the south-east that of the upper gorge country into which it gradually passes. In the more inhabited typical outer plateau country two distinct types of terrain are met with: (i.) gravel land and (ii.) grassland.

#### *Gravel lands.*

The gravel lands are familiar to all who have travelled the trade route between India and Lhasa. There are numerous small lakes. The flora is sparse. On the low ranges which rise from the plateau where there is shelter, and again by streams, it is more varied. Grassland plateau country is met with to the north-west of Batang, though this region might also be regarded as part of the river gorge country. Much of the pasture occupies ancient lake beds which have dried up, and the small streams flow in wide shallow troughs. The main grassland area, however, is in N.E. Tibet.

Throughout the region described there is a shortage of rain (which falls mostly in summer), a dry atmosphere, and severe winter. The vegetative season is short, even in the most favoured localities, and the high winds are hostile to woody vegetation. The snow-line varies between 17,000 and 18,000 feet. The total area of the outer plateau is about 300,000 square miles.

Taking Professor R. S. Kashyap's collection as a basis\*, and adding to the 340 species enumerated by him, 178 (less 10 endemic on the Chang Tang) from Hemsley's list not recorded in the above, and 33 species collected by myself on the plateau, we have a total of 541 species recorded from the outer plateau. This is certainly too low. Many of these plants are known also from the river gorge country.

\* Presidential Address, Nineteenth Indian Science Congress, 1932.



*Grassland.*

The north-east corner of Tibet, bordering on the Chinese province of Kansu differs in some ways from all other parts of the country. It is a bleak plateau region, traversed by high rocky wooded ranges of limestone mountains forming part of the watershed between the Yangtze and Yellow River systems. The drainage is therefore external to the Yellow River and its tributaries. The plateau is covered mainly with grass, forming a rich grazing country; but there is coniferous and broad-leaved forest on the ranges, as well as a fairly rich alpine flora. The principal rivers are the Tao, Yellow River, Sining River, and the rivers which feed the Koko Nor.

The alpine flora resembles that of the outer plateau rather than that of the Chang Tang; indeed, the grassland plateau may be regarded as the eastward slope of the outer plateau, where it slants down towards Chinese Tibet. It has been extensively explored by the Russians, especially by Prejevalsky in 1871-73. Mr. R. Farrer and Mr. W. Purdom collected plants here in 1913-14. My own experience of this region is confined to a journey through Kansu and up the valley of the Tao River in 1910, whence I passed southwards into Szechuan and Chinese Tibet. Recently Mr. J. Rock, an American, has travelled and collected there.

On the plateau proper there is no woody vegetation, and in this respect it resembles the more typical outer plateau. Forest is confined to the valleys and to a belt on the higher ranges. The alpine flora is rich in plants, though comparatively poor in species. *Meconopsis*, *Primula*, *Gentiana*—all the well-known Sino-Himalayan genera—occur. This is the home of *M. quintuplinerva*.

The climate is severely continental, the winters long and hard. The elevation of the grassland plateau is lower than that of the average outer plateau. The Koko Nor itself stands 10,700 feet above sea-level. The tops of the ranges attain some thousands of feet higher, but probably rarely exceed the snow-line, which stands at about 19,000 feet. The total area of the grassland plateau, a specialized part of the outer plateau, is about 150,000 square miles, or half the total area.

## V. THE RIVER GORGE COUNTRY.

The river gorge country comprises all that part of Tibet lying between the great gorge of the Tsangpo in the south-west (longitude  $92^{\circ}$  E.) and the valley of the Yangtze in the north-east (longitude  $98^{\circ}$  E.) between the twenty-eighth and thirty-second parallels. Thus it includes the provinces of Kongbo and Takpo in part, Pome, Pemako, Poyul, and Zayul, together with the districts of Nagong, Pashu, Chamdo (in part), Tsarong, and most of what is vaguely called Kam. In the south the river gorge country marches with the frontiers of Burma and Assam, in the east with the frontiers of Yunnan and Szechuan—that is, Chinese Tibet.

This part of Tibet, comprising about 10,000 square miles, or one-eighth of the whole, is drained by rivers which rise on the outer rim of the Chang Tang and

flow for hundreds of miles across the outer plateau before they begin to cut out deep gorges for themselves, separated from one another by high but narrow mountain ridges—with peaks rising far above the snow-line. Towards the north-east the rivers are only beginning to converge as they leave the outer plateau. Between lat.  $26^{\circ}$  and  $30^{\circ}$  they are all flowing nearly due south, parallel to, and close to, one another. In the south-east they diverge once more, where the river gorge country passes gradually into the tangled mountain systems of Assam, Burma, and Yunnan.

The whole region is a world on edge; yet it, too, was once part of the plateau and still shows abundant evidence of its original plateau structure. Tibet was then buried under an ice-sheet, from which many great glaciers flowed south. Since the disappearance of the ice-sheet and the retreat of the glaciers, the rivers have been gradually gnawing their way back into the plateau by head erosion, so that the outer plateau is ever encroaching on the Chang Tang. At the same time the rivers, loaded with rock filings, have been busy cutting gorges for themselves through the containing walls thousands of feet below the ancient plateau level; but the river gorge country is now scarcely encroaching on the outer plateau, because the rivers no longer have the same corroding power\*.

The principal rivers are, from west to east: the Tsangpo with its big affluent the Po-Tsangpo and its smaller affluents the Gyamda, Chimdru, and Nyang Rivers. (The Tsangpo, called Dihang in the Abor Hills, is the main stream of the Brahmaputra, which it joins at Kobo at the head of the Assam valley.) The two branches of the Lohit called the Rong Tö chu (or Zayul Ngu chu) and the Zayul chu; the Salween and its big affluent the Wichu and several smaller affluents. The Mekong; and the Yangtze, with several big affluents. The headwaters of the Taron or Irrawaddy also rise just within this region. Beyond the Yangtze lies Chinese Tibet really an eastward extension of the river gorge country. In Western Tibet the Indus and Sutlej flow westward across the outer plateau. The river gorge country is sharply divided into two distinct regions by a great mountain range into (1) the lower gorge country south of the great snow range, and (2) the upper gorge country north of the great snow range. It is the only abrupt transition in Tibet. Where the great snow range is the Great Himalayan itself, the only Tibetan territory which lies south of it is the Chumbi valley. East of Namcha Barwa, however, the provinces of Pemako and Zayul lie almost entirely south of the Himalayan extension†.

\* Mr. I. H. Burkill has remarked that 'very tempestuous weather must have occurred . . . between the icefields and the Equator owing to the proximity of the one to the other. Therefore there was water in plenty for cutting the gorges' (Proc. Linn. Soc., Sess. 146, 1933-4, p. 113).

† Small scale maps of S.E. Tibet show no such extension of the Great Himalayan range eastwards. That the range, however, originally existed is to be inferred from the alignment of the high peaks, as well as from the distribution of plants and other considerations set forth at the beginning of this paper.

(1) The lower gorge country enjoys a warm climate in the deep valleys, though the mountains rise to considerable heights and are snow-clad for the greater part of the year. In the west and south the river gorges are hot in summer, but cold in winter. Rain or snow falls at all seasons, and the atmosphere is always moist. Deep snow lies at 10,000 feet for half the year, chilling the air and precipitating rain, so that the summers are very wet. The snow-line stands at about 16,000 feet, but permanent snow-beds occupy the deep glens far below this, and remnant glaciers, though small, are found on all the main ranges, one descending to 8,000 feet in Zayul. The valleys are, of course, filled with forest, which ascends far up the flanks of the mountains. Southwards, temperate forest passes gradually into the hill jungle of the Indo-Malayan region; eastwards it passes into Conifer forest. In the east the rainfall is less and the atmosphere drier.

The alpine and sub-alpine flora of the lower gorge country spreads far beyond the boundaries of Tibet, down the long high ranges which run southwards into Burma. But this alpine flora is distinct from the alpine flora of the upper gorge country.

The lower gorge country, though politically part of Tibet, is completely cut off from the real Tibetan plateau country (including the upper gorge country), and is not *geographically* part of Tibet at all. Even at the time of the glacial epoch, placed as it is south of the great containing wall, it must have stood at a lower level than the Tibetan plateau, of which it was an appendage. It was probably uplifted at the same time as the Burma-Yunnan ranges, and was not much affected by the Himalayan earth movements. It is occupied by peoples of Tibeto-Burman (i.e. non-Aryan) descent, but not by true Tibetans, who cannot live in so moist a climate.

(2) The upper gorge country is drier and colder, with a climate which, on the average, approaches more nearly to that of the outer plateau. Only in the few main river gorges are the summers hot; in the Alps the winters are severe. High winds are as much a feature here as on the plateau, but in the gorges they are scorching winds. The summers are short, with ample, but not excessive, rain; the winters long and dry. Consequently the upper gorge country is much poorer in woody species than is the lower gorge country, and over large areas forest is entirely lacking, and even trees are rare. Nevertheless, there are great stretches of Coniferous forest, especially in the neighbourhood of the great snow range. Where the rivers begin to diverge north of 29° there are broad stretches of pastureland between them. In the Tsangpo valley the beginning of forest marks the transition from plateau to gorge country. Glaciers, though small, are very numerous (in the form of hanging glaciers) on all the main sierras, the snow-line standing at about 18,000 feet.

Westwards and northwards the upper gorge country passes gradually into the outer plateau. Eastwards it passes into Chinese Tibet—a special development of the river gorge country. Southwards it is bounded by the

great snow-range, which, being widely breached between the Tsangpo and the Yangtze, has allowed the development of the lower gorge country below.

So rich and varied is the flora of the river gorge country, corresponding to the great diversity of climate and soil, that it will be convenient to go into it in rather more detail; for it is no exaggeration to say that three-quarters of the entire Tibetan flora (excluding Chinese Tibet) is found here. Taking first the upper gorge country, which nowhere, not even in the gorges, lies below 9,000 feet, we have the following:—

- 9,000–12,000 feet . . . . . Arid river gorges. Shrub flora with a few trees round the villages. *Picea*, Juniper, Poplar: shrubs include *Papilionaceae*: *Aster*: *Caryopteris*; *Plectranthus*; *Ceratostigma*. Herbs include *Amphicome arguata*: *Eremurus*, *Primula sikkimensis*.
- 12,000–14,000 feet . . . . . Sub-alpine region. Shrub belt. Rhododendrons in limited variety: *Berberis*: *Lonicera*, *Ribes*, *Clematis*, *Rosa*. Alpine flowers include *Incarvillea* and *Stellera chamaejasme*; *Compositae* in vast numbers and great variety. *Cruciferae* and *Ranunculaceae* come next. A few *Labiatae* (*Dracocephalum*). Great numbers of *Pedicularis*. In moist places *Primula tibetica*.
- 14,000–15,000 feet . . . . . High alpine region: Herbaceous zone; Larkspurs, *Asters*, *Meconopsis horridula*, shrub belt with "lapponicum" and "Anthopogon" Rhododendrons, dwarf *Hippophaë*. In moist places *Uremanthodium*.
- 15,000–17,000 feet . . . . . High alpine region. Scree: alpine turf: glacier sand flats: boulder slopes. Dwarf alpine plants: "Nivalis" *Primulas*: rosette plants—*Crepis*, *Gentians*, *Lagotis*.
- 17,000–18,000 feet . . . . . High alpine region. A few specialized plants—*Delphinium Brunonianum*. *Saussurea*; *Primula* sp.

In the lower gorge country the average altitude is high, although in the Salween valley and in Zayul it drops down so low as 5,000 feet. There being no rain screen between the plains of India and the great snow-range, the country receives most of the benefit of the monsoon and is covered everywhere, except on the highest tops, with forest. Here we can recognize the following sequence:—

- Below 5,000 feet . . . . . Zayul River only: *Pinus Khasia*.
- 5,000– 8,000 feet . . . . . Temperate evergreen forest as in the Zayul River gorge: *Pinus Khasia* and *P. excelsa*, with Oaks, Maples, and *Ilex*. Temperate rain forest: *Magnolia Campbellii*, *Michelia lanuginosa*.
- 8,000–10,000 feet . . . . . Rhododendrons and conifer forest mixed with broad-leaved trees. Rhododendrons in variety: *Picea* and *Taxus*, *Abies Pindrow*, *Magnolia globosa*.
- 10,000–12,000 feet . . . . . Fir forest. *Abies Webbiana* with Rhododendrons and deciduous shrubs as undergrowth.
- 12,000–14,000 feet . . . . . Rhododendron scrub: gregarious species but some variety. Alpine meadow with *Nemocharis*, *Primula Agleniana*, *Meconopsis betonicifolia*.
- Above 14,000 feet . . . . . Alpine turf: scree: cliffs and ice-worn rock slopes. *Primula Dickiana*, *P. Valentiniana*.

Comparing the two sequences :—

	Lower.	Upper.
Below 5,000 feet . . . . .	<i>Pinus Khasia.</i>	.....
5,000- 8,000 feet . . . . .	Temperate evergreen forest.	.....
	„ rain forest.	.....
8,000-10,000 feet . . . . .	Rhododendron-Conifer forest.	Arid river gorges.
10,000-12,000 feet . . . . .	Fir forest : <i>Abies</i> and <i>Rhododendron.</i>	„ „
12,000-14,000 feet . . . . .	Rhododendron scrub.	Sub-alpine shrub belt.
	Alpine meadow.	Alpine flowers.
Above 14,000 feet . . . . .	Alpine turf : screes.	Alpine : herbaceous zone, with small shrubs.
15,000-17,000 feet . . . . .	.....	High alpine region, with dwarf alpenes.
Above 17,000 feet . . . . .	.....	Specialized high alpenes.

Although altitude alone is not a good basis for subdividing a flora (many species having a considerable vertical range) and the real test for a plant being atmospheric humidity, yet, with altitudes running into thousands of feet and atmospheric humidity varying with the altitude, this easily ascertained factor does for a rough guide. Thus it will be seen that there are two sharply contrasted floras in the river gorge country: the upper related to the plateau flora, the lower to the sub-tropical Indo-Malayan flora.

The most remarkable feature of the river gorge country is the wealth of alpine flowers and dwarf shrubs in the higher zones—this is no less remarkable in the lower than in the upper gorge country. But the lower gorge country is also remarkable for the variety of trees and shrubs it possesses. Between 6,000 and 12,000 feet forest prevails. In the lowermost zone 6,000 to 8,000 feet is temperate rain forest, especially developed in the gorge of the Tsangpo. All the trees are swathed in moss, and epiphytes including Rhododendrons abound. This forest is difficult to penetrate, not only by reason of the steepness of the slopes, but also because of the dense undergrowth of *Arundinaria* and other plants. Between 8,000 and 10,000 feet is the zone of tree Rhododendrons, with Oaks, Hollies, Maples, Araliaceae, and mixed Conifers. Above the temperate forest belt silver fir forms extensive forests by itself, with an undergrowth of Rhododendrons and deciduous shrubs.

As for the upper gorge country both mountains and valleys are more elevated, and the whole country has a more arid and typically Tibetan appearance. The scenery here is perhaps the grandest in all Tibet.

From what has been said, it is clear that the flora of Tibet becomes progressively richer and more varied as one travels south-eastwards from the heart of the Chang Tang, across the outer plateau, into the river gorge country, where many types of plant association are met with. The Chang Tang is practically a desert. The outer plateau is alpine. The river gorge country, taken as a whole, is one of the botanical treasure houses of the world.

Two points concerning the plateau flora, and I include here the upper gorge country, are worth noting :—(1) Its lateness, (2) its high average altitude.

It is a late summer and autumn flora—July to October. It needs must be frost-resisting. Many alpine—and this applies also to the lower gorge country—have persistent corollas, which may change colour as the capsule ripens, but otherwise are little altered. Even certain Polypetalæ, including several species of *Saxifraga*, *Clematis tangutica*, a *Trollius*, and an *Arenaria*, have these persistent corollas. It is very conspicuous amongst the late-flowering Gentians, and in one of the highest flowering plants, *Aconitum Brunonianum*, which is never found below 16,000 feet and may occur at 18,000 feet and over. Gentians may be found at 10,000 feet altitude and even higher in full bloom so late as the last week in November. The corolla is frozen to the consistency of parchment at night and thawed out by day. This raises the question of seeds and low temperature. Seeds of many alpine are alternately frozen and thawed, moistened and dried, before they are buried under the snow. Many pass the winter still in their capsules under the snow. I have observed the seeds of *Nomocharis* germinating in their capsules in June after being six months under the snow.

The absence of bulbous plants on the outer plateau, and even throughout the upper gorge country, is at first sight surprising. But the soil is cold as well as dry. A few species of *Allium* and *Lloydia* occur. Similarly, there are few Irises in the dry regions of Tibet. Aromatic foliage and scented flowers are characteristic features.

#### CONCLUSIONS.

Mr. W. B. Hemsley, in the paper already referred to, says: 'No elaborate arguments are required to prove that the Tibetan is a derived Flora—that is to say, derived since the Tertiary period; and its composition is so largely Himalayan that there can be little doubt as to its origin'.

Mr. C. V. B. Marquand \* says:—'The material available now makes it quite clear that one homogeneous flora extends across from Sikkim to western China, and the whole of the Eastern Himalaya, South-eastern Tibet, and western Szechuan as well as the upper portion of Yunnan should be considered as one botanical area.'

I have endeavoured in this paper to prove the correctness of these views, to reinforce and extend them. I consider, however, that the Tibetan flora has been derived since the Pleistocene; and that the whole of Tibet, together with the Himalaya west of Sikkim and the Karakorum to the north-west, must be included in the one botanical or floral region. I have tried to show not only why, from the evidence of plant distribution now available, this is the right view, but also how this distribution has been brought about. This floral region may be called Sino-Himalaya. As to why I have detached the Tibetan plateau from its old allegiance to the Central Asian region—apart from the obvious relationship between the plateau flora and the mountain ranges to the south and south-east—I will add a few words.

\* Linnean Society's Journal, Botany, no. 321, April 1929.

The Central Asian floral region is characterized by its richness in halophytes, such as *Chenopodiaceae*, *Astragalus*, especially shrubby species, *Oxytropis*, *Polygonum*, and *Rheum*. It is also rich in bulbous plants and in *Plumbaginaceae*, *Umbelliferae*, and some others.

The plateau flora of Tibet comprises, so far as is known, 541 species of flowering plants. *Chenopodiaceae* number 12 species (one doubtful), *Umbelliferae* 12, and *Plumbaginaceae* 2. Of the remaining genera, *Astragalus* has 12 species, *Oxytropis* 12, *Polygonum* 12, *Rheum* 1. If we count these all as typical Central Asian plants, we get a total of 63 species or 11·6 per cent. of the known flora. Not a very large proportion! Against that must be set the fact that the plateau flora is rich in species of *Ranunculus*, *Draba*, *Corydalis*, *Caragana*, *Potentilla*, *Saxifraga*, *Sedum*, *Artemisia*, *Saussurea*, *Allium*, *Gentiana*, *Pedicularis*, and *Salix*, none of which are especially characteristic of the Central Asian region properly understood. All, or nearly all, of them occur in western China or on the higher ranges of south-eastern Tibet. Nor can it be contended that the Tibetan plateau is merely a poor and desert portion of the Central Asian region. Central Asia is a desert; its flora is poor.

Moreover, the true Central Asian region lies thousands of feet lower than the plateau, and is separated from it by huge escarpments. The climate is very different, though it produces the same result—namely desert; its geological history is different.

What was happening in Central Asia when the ice-belt which stretched across southern Tibet isolated it we can only conjecture; but clearly it was not much more isolated then than it is now. I have shown how the Himalayan uplift is prolonged eastwards, an important point in unravelling the floras of south-eastern Asia. The distribution of plants on the Sino-Tibetan ranges had long ago led me to this solution; but its proof rests mainly on geological and geographical evidence only now available\*.

\* See 'The Himalaya east of the Tsangpo.' 'Geographical Journal', November 1934.

#### EXPLANATION OF MAP 2

The principal groups of snow peaks seen by the writer during the years 1911, 1913, 1921–22, 1924, 1931, 1933, are shown shaded. There is every reason to suppose that they formed a continuous range, or ranges, of ice clad mountains. The ice front (dotted line) at the time of maximum glaciation is obtained by joining up the furthest points in the river gorges where unmistakable evidence of ice action was observed. The southern extensions enclosed by thin dot and dash lines show the areas on the mountain ranges where ice action was observed beyond the furthest points in the gorges.





## The British Robertsonian Saxifrages.

By H. W. PUGSLEY, B.A., F.L.S.

(PLATES 6 &amp; 7)

[Read 9 May 1935]

IN 1924 I sent to the Watson Botanical Exchange Club specimens of *Saxifraga umbrosa* L., derived from plants which I had collected in 1919 in its well-known station in Heseldon Glen, Yorkshire. With the specimens I included a note (inserted in the Club's Report and reprinted in Journ. Bot. lxiv, p. 19) drawing attention to the fact that the Yorkshire plant agreed with the Pyrenean form of the species, while the common Irish variety resembled that found in Asturias and Portugal. Since that date I have seen *in situ* the Pyrenean plant in the mountains above Luchon, and the Irish one in Kerry and Wicklow; and for some years all of these forms, together with 'London Pride', have grown in my garden. I have likewise collected the *S. Geum* of British botanists in the Pyrenees, as well as in Ireland, where I observed also some interesting intermediate forms such as have been referred to *S. hirsuta* L.

It is very clear that the Irish *S. umbrosa*, identified with *S. punctata* L. by Haworth and David Don, differs widely from the plant of Yorkshire and the Pyrenees, and equally ambiguous whether there exists in Ireland a species *S. hirsuta* L. distinct from *S. Geum*. In his 'Flora of Kerry' Dr. Scully discusses the latter question at great length, and concludes that the Irish *S. hirsuta* is composed entirely of varying hybrids between *S. Geum* and *S. umbrosa*. As all of these plants bear Linnean names, I will attempt to demonstrate the original identity of each of them, with some prefatory remarks on their treatment before the time of Linnaeus.

## PRE-LINNEAN TREATMENT OF THE GROUP.

It is somewhat remarkable that these attractive plants, which are not uncommon in the Pyrenees, were apparently unknown to the writers of the sixteenth century. There is no reference to them in the works of Lobel, Clusius or Gerard, and they seem to be omitted from Caspar Bauhin's 'Pinax'. Linnaeus's citation from the 'Pinax' under *S. Geum* (Sp. Pl. p. 401) and that from Clusius on which it is based (Hort. Cliff. p. 167) are erroneous, for the plant intended by these early authors is *S. stellaris* L. No other synonym cited by Linnaeus for plants of this group is earlier than the latter part of the seventeenth century. The first record that can be traced is in Parkinson's

'Paradisus' (1629), where (pp. 232 & 233, f. 5) we find '*Sedum serratum flore rubente maculato*. The Prince's Feather'. Parkinson remarks, 'It is said to grow in Germany, Hungarie, Austria, the Alpes . . . will abide in gardens reasonable well . . . in shadowie places'. The plant was apparently not well known to Parkinson and his figure is crude. In the 'Theatrum Botanicum' (1640) the 'Prince's Feather' is again figured (p. 738) under the name of *Sedum montanum serratum guttato flore*. This second figure clearly depicts the Pyrenean *Saxifraga umbrosa*, showing well the oblong, crenate foliage and densely ciliate petioles. How's 'Phytologia', p. 111 (1650), mentions as '*Sedum serratum, sive Umbilicus Veneris alter* Math. *Cotyledon altera* 4 Clus. Hist. The Prince's Feather' what is probably the same plant.

Fifteen years later two forms of this group are included in a list of plants cultivated at Paris in D. Jonequet's 'Hortus Regius' (p. 161). They are *Sanicula montana crenata umbilico pallido* and *S. m. c. umbilico rubro* (= *Sedum montanum serratum guttato flore* Park.). The second species is probably identical with Parkinson's 'Prince's Feather', and the pale capsule of the first seems to indicate the modern *S. Geum*, of which it is the earliest-known record. Ray (Hist. ii, p. 1046 (1688)) adopts the name *Cotyledon sive Sedum serratum latifolium montanum guttato flore* for Parkinson's plant, of which he says two varieties are grown, one with larger flowers than the other. Its origin was evidently unknown to him, for he writes: 'In hortis nostris frequentissime est; ubi tamen sponte oritur nobis nondum constat, est autem proculdubio montium incola'. *Sanicula montana crenata umbilico pallido* is also mentioned in the 'Historia,' but without any original information.

In Tournefort's 'Elémens de Botanique', i, p. 218 (1694), four of these plants appear in the enumeration of the species of *Geum*. They are:—(1) *Geum folio circinato, pistillo floris pallido* (*Sanicula montana crenata umbilico pallido* H. R. P.), (2) *G. folio circinato acute crenato, pistillo floris rubro*, (3) *G. folio subrotundo majori, pistillo floris rubro* (*Sedum montanum serratum guttato flore* Park.), and (4) *G. folio subrotundo minori, pistillo floris rubro*. The first two species, with circinate leaves, seem to be *Geum*-like plants; the last two, with subrotund leaves, allies of *S. umbrosa*; the second and fourth are new. The four species reappeared in 1697 in Magnol's 'Hortus Regius Monspelienensis', p. 87, where accurate detailed descriptions of the second and fourth are furnished with fairly good figures supplied by Tournefort. No. 2 is a Pyrenean plant akin to *S. Geum*, characterised by red-spotted flowers and ruddy capsules; no. 4, obtained in the Cantabrian Mountains, is a more compact form of no. 3. The two plants described, which are of especial importance because later two of Linnaeus's species were founded upon them, are included in a Supplement to Ray's 'Historia', p. 508 (1704).

In the same year (1697), according to Dr. Scully, a plant of this group was discovered in Ireland (on Mangerton, in Kerry) by Dr. T. Molyneux, and it was again found there in 1699 by Llwyd, who also collected a form of *S. Geum*. There are specimens of these plants in Buddle's collection in the Sloane

Herbarium (H.S. 124/17). Three forms of these plants are figured on pl. 61 of Petiver's 'Herbarium Britannicum' (1715), under the names of 'Garden Pride' (Parkinson's original plant), 'Round Pride' (*S. Geum*), and 'Irish Pride' (the common Irish form). Threlkeld ('Synopsis Stirpium Hibernicarum' (1727)) states that *Sedum montanum serratum guttato flore* grows plentifully on Mangerton, and quotes as English names 'London Pride, None-so-pretty or Prince's Feather'. It may now be seen that at least four forms belonging to the Robertsonian Section of *Saxifraga* had been brought into cultivation before the time of Linnaeus. As *S. Geum*, *S. hirsuta*, and *S. punctata* were described in the first edition of 'Species Plantarum', and *S. umbrosa* in the second edition, I will proceed to take them *seriatim*.

#### THE LINNEAN SPECIES.

##### SAXIFRAGA GEUM L. (Pl. 6.)

*S. Geum* is described in Sp. Plant. p. 401 (1753) thus:—

- ' 11. *S. Geum*. *S. foliis cordato-ovalibus retusis cartilagineo-crenatis, caule nudo paniculato.* Hort. Cliff. 167\*.

*Geum foliis petiolatis retusis, ora cartilaginea, serrata, caule ramoso.*  
Hall. Helv. 400.

*Sanicula montana rotundifolia minor.* Bauh. Pin. 243.

*Hab. in albis helveticis, pyrenaicis.'*

Linnaeus here furnishes no diagnosis or description, but adopts the diagnosis of his earlier work, Hort. Cliff., in which, however, he now inserts the additional words 'cartilagineo' and 'paniculato'. The account of this plant in Hort. Cliff. is a lengthy one, and it is divided into four forms, the first two of which have several synonyms. The forms are:— $\alpha$ , *Geum folio circinato, pistillo floris pallido*, Tourn. Inst. 251;  $\beta$ , *G. folio subrotundo minore, pistillo floris rubro*, Tourn. Inst. 251;  $\gamma$ , *G. folio oblongo crenato, fructu et cauliculis ruberrimis, flore pallido rubris guttatis aspersis* Boerh.; and  $\delta$ , *Sanicula montana rotundifolia minor hispanica*, Raj. Hist. 1047. The species is said to grow in the Swiss Alps and Irish Mountains. Linnaeus adds that the plant is ambiguously described by authors and not well figured, and concludes with a description stating that its leaves are all oval, cordate at the base, and crenate with rounded, almost imbricate lobules, and its flowers white and usually spotted. He notes, however, that the shape of the leaves may vary to oblong, without cordate base, or to orbicular and cordate. The species, as here conceived, obviously includes different plants, and vars.  $\beta$  and  $\gamma$  seemingly belong to *S. umbrosa*. The synonyms from Haller and Caspar Bauhin cited in Sp. Plant. apparently belong to *S. cuneifolia* L. and *S. stellaris* L. respectively, and are quoted in error by Linnaeus.

The Linnean Herbarium contains a specimen of *S. Geum*, labelled by Linnaeus, which is shown in Dr. Jackson's Index to have been placed there before 1753.

It appears to have been obtained from the Hortus Cliffortianus, and on the back of the sheet, in Linnaeus's handwriting, is '*Geum folio circinato, pistillo floris pallido*', indicating that he regarded it as the var.  $\alpha$  of Hort. Cliff. The specimen is a good one. Its leaves are broadly oval, cordate-based, nearly truncate, thick, glabrous, and markedly cartilaginous-crenate, with the rounded crenatures small and subimbricate. It differs greatly from the Irish and Pyrenean *S. Geum* of modern botanists and is nearer to the Pyrenean *S. umbrosa*, from which it is separable chiefly by its longer and less flattened petioles and cordate-based foliage. Among the plants of Hort. Cliff. in Herb. Mus. Brit. there are three specimens referable to this group, one of which, labelled '*Geum folio circinato, pistillo floris pallido*', is identical with the plant of the Linnean Herbarium. The two specimens obviously agree both with the diagnosis in Sp. Plant. and with the description in Hort. Cliff. The original *S. Geum*, therefore, was a plant presumably cultivated in Cliffort's garden at Hartecamp, where it was known to Linnaeus, and the specimen in the Linnean Herbarium must be held to be the nomenclatural type. Whence the plant was obtained by Cliffort is unknown, but it is significant that both in Hort. Cliff. and Sp. Plant. Linnaeus mentions the Swiss Alps as the first habitat of the species. As the synonyms in Sp. Plant. refer to two different species, the name should be cited as '*S. Geum* L. excl. syn.'

It will be shown that Linnaeus subsequently changed his conception of *S. Geum*, but this does not invalidate his original account or the application of the specific name.

#### SAXIFRAGA HIRSUTA L.

This species immediately follows *S. Geum* in Sp. Plant. thus :—

- '12. *S. rotundifolia*. S. foliis reniformibus dentatis, caule nudo paniculato.  
Geum folio circinato acute crenato, pistillo floris rubro. Magn. Hort.  
87, t. 87.

*Hab.* in alpinis pyrenaicis, sibiricis.

*Facies* *S. rotundifoliae*, sed caulis nudus.'

The specific epithet '*rotundifolia*' was evidently printed through a clerical or printer's error, for *S. rotundifolia* is no. 19 of Linnaeus's *Saxifragae* in this work, and is contrasted here with the present species. In Linnaeus's own copies of Sp. Plant. '*rotundifolia*' is struck out and '*hirsuta*' substituted in manuscript. The mistake was corrected in the tenth edition of '*Systema Naturae*' (1759), where (p. 1026) under *Saxifraga* we read '12. *hirsuta*. S. fol. cordato-ovalibus obtusiuscule dentatis, caule nudo paniculato'. It will be noticed that the diagnosis has been modified, '*reniformibus dentatis*' becoming '*cordato-ovalibus obtusiuscule dentatis*'. A change from '*cordato-ovalibus retusis*' to '*obcordato-ovalibus*' also appears here in the corresponding diagnosis of *S. Geum*.

In the second edition of Sp. Plant. a further modification takes place, and the original diagnoses of *S. Geum* and *S. hirsuta* are transposed, so that we get :—

- ' 16. *S. hirsuta*. *S. foliis cordato-ovalibus retusis cartilagineo-crenatis, caule nudo paniculato*.  
*Geum folio circinato acute crenato, pistillo floris rubro*. Magn. Hort. 87, t. 87.  
 Hab. in pyrenaeis.  
 Affinis *nimum sequenti*, sed folia ovalia nec reniformia.
17. *S. Geum*.—*S. foliis reniformibus dentatis, caule nudo paniculato*.  
*Sanicula montana rotundifolia minor*. Bauh. Pin. 243.  
*Sedum montanum rotundifolium minus album non guttatum*. Moris. Hist. 3, p. 478, f. 12, t. 9, f. 12.  
 Hab. in alpinis Europae.'

Dealing with *S. hirsuta*, it will be seen that Syst. Nat. ed. 10 should be cited for the species, owing to the misprinting of the trivial 'rotundifolia' in Sp. Plant. The valid diagnosis of *S. hirsuta* may therefore be said to be '*S. foliis cordato-ovalibus obtusiuscule dentatis, caule nudo paniculato*', although this was not the original conception of Linnaeus. The '*obtusiuscule dentatis*' becomes '*retusis cartilagineo-crenatis*' in Sp. Plant. ed. 2, but the synonymy remains unaltered, the species being still founded solely on Magn. Hort. 87, t. 87, as in Sp. Plant. ed. 1. As treated by Linnaeus in 1762, *S. hirsuta* is associated with *S. Geum*, the form of the foliage constituting the essential difference.

There is no type-specimen of *S. hirsuta* in the Linnean Herbarium. A sheet labelled '*hirsuta*' by Linnaeus is present there, but it was apparently acquired after 1767. This sheet shows a panicle, and a detached leaf which does not agree with the diagnosis but recalls the form of *S. umbrosa* known as the 'London Pride' of modern gardens. It thus becomes necessary to rely mainly on the citation from Magnol's Hort. Monsp. for the determination of the species. It fortunately happens that Magnol's account of his *Geum folio circinato acute crenato, pistillo floris rubro* is so precise and well illustrated that the plant intended is unmistakable. It is a Pyrenean form that produces nearly round, crenate foliage, pilose above and glabrous below, borne on long pilose petioles. It has the characteristic inflorescence of the group, with white petals spotted with red. The figure, supplied by Tournefort, shows a *Geum*-like plant with rotundate leaves, as broad or broader than long, cordate below, and with coarsely dentate-crenate margins. The petioles and scape are relatively slender. This must be regarded as typical *S. hirsuta*.

The *S. Geum* of Sp. Plant. ed. 2 is distinguished from *S. hirsuta* by its reniform, i.e. broader, foliage. The fresh synonym introduced from Morison's 'Historia' is contradictory, for, while the plant with unspotted flowers may be of doubtful identity, the figure cited is clearly the modern *S. Geum* with spotted petals. On examining a number of Pyrenean and Irish specimens of *S. Geum* auct. it may readily be seen that the shape and cutting of the leaves varies considerably, sometimes on a single individual plant, and Magnol's original description '*fere rotunda*' (l.c.) is accurate in a general sense. The *S. Geum*

of Sp. Plant. ed. 2 is therefore essentially different from the original *S. Geum* and little more than a broad-leaved form or variety of *S. hirsuta*. Grenier and Godron (Fl. Fr. i, p. 639), Wilkomm and Lange (Fl. Hisp. iii, p. 125) and Coste (Fl. Fr. ii, p. 132) adopt the name *S. hirsuta* L. for the species, and add a variety *Geum*, with foliage hirsute on both surfaces. These authors commonly cite the second edition of Sp. Plant.

Linnaeus rightly attributes a Pyrenean origin to *S. hirsuta*, and it seems possible from the addition of 'alpinus sibiricus' in his account of 1753 that he was acquainted with the somewhat similar Siberian plant of Gmelin's which later was wrongly identified with *S. punctata* L.

#### SAXIFRAGA PUNCTATA L. (Pl. 7.)

The original description of this species (Sp. Plant. p. 401) runs :—

- '13. *S. punctata*.—*S. foliis obovatis dentatis petiolatis, caule nudo paniculato. Sedum bicornis serratum, pallidior folio rotundior, floribus punctatis. Moris. Hist. 3, p. 478, f. 12, t. 9, f. 17. Hab. in Sibiria.*'

This is repeated in the second edition (p. 574), with a modification of the diagnosis to '*S. foliis subrotundis dentatis longius petiolatis, caule nudo*'; and a description is appended: '*Folia subrotunda, dentibus incisa, ut fere lobata absque ora cartilaginea, minime retusa, dentibus acutis. Petioli laeves, foliis triplo longiores, superne sensim dilatati in folium. Flores minores quam in S. Geum, fere inferi*'.

This species is represented in Herb. Linn. by a fair specimen, which was present before 1753 according to Dr. Jackson's Index. It is labelled '*punctata*' by Linnaeus, and 'not of D. Don' is added in Smith's hand. On the back of the sheet is written: '*S. foliis cordato-ovalibus crenatis emarginatis caule nudo. H. C. Gmel. perperam. Saxifraga 3. Hort. Cliff.*'. The specimen agrees with the diagnosis and especially with the more precise description, and must evidently be accepted as the specific type. At first sight it recalls the foliage of the common Irish form of *S. umbrosa*, but the petioles are longer and the laminae, though of similar outline, are of a widely different texture, less coriaceous, and without any cartilaginous margin. Whether the synonym cited from Morison is conspecific is doubtful. *S. punctata* clearly belongs to the generic Section *Boraphila* Engl. and is quite distinct from the group under discussion (*Robertsonia* Haw.).

Since the time of Linnaeus *S. punctata* has been curiously misidentified. At an early date it seems to have been associated with Gmelin's *S. foliis cordato-ovalibus crenatis emarginatis, caule nudo* (Fl. Sibir. iv, p. 151 (1769)), which has the aspect of *S. Geum* auct. Sternberg (Revis. Saxifragarum, p. 18 (1810)) describes the Siberian *S. punctata* as with '*foliis reniformibus*', and in his Supplement (t. 4) it is figured with reniform, toothed leaves, and resembles *S. Geum*. Don (Mon. Saxifr. in Trans. Linn. Soc. xiii, p. 349 (1822)) remarks that Sternberg in his monograph has described the Siberian *S. Geum* as *S. punc-*

*tata* L., and himself treats *S. Geum* as a Siberian plant. In later works, including Engler and Irmscher's *Saxifrageae* in 'Pflanzenreich', iv, 117, i, p. 9, the Siberian plant, with reniform leaves, resembling *S. Geum* in habit, has continued to be described, following Sternberg, under the name of *S. punctata* L.; and it is now known to be a widely spread species not only in Siberia but in North America. Although similar to *S. Geum* in general aspect, it is a radically different plant and is no doubt correctly placed in the generic Section *Boraphila* Engl. But it is almost equally distinct from the original *S. punctata* L., which has entirely different foliage. So far as has been traced, its valid name is *S. aestivalis* Fisch. & Mey., Ind. Sem. Hort. Petrop. i, p. 57 (1835). These authors give an accurate description and clearly distinguish it from *S. Geum*.

The true *S. punctata* L. was re-described by Willdenow in Sp. Plant. ed. 4, p. 645 (1799), as *S. davurica*. Willdenow, who does not seem to have understood *S. punctata*, founded his new species on '*S. punctata* Pallas, itin. 3, app. no. 91, t. P, f. 2', giving as a diagnosis '*S. foliis cuneiformi-rhombeis apice dentatis glabris petiolatis, caule nudo*', with the habitat '*Alpibus Davuriae*'. There is an authentic example of this plant in Herb. Mus. Brit. from Pallas's herbarium, labelled '*Hb. Pallas ex alpibus Davuriae*', and annotated by Smith '*S. punctata* Linn. et etiam Pallas in itin. collata cum Herb. Linn.'. It may be seen at once, upon comparison, that this plant is identical with the Linnean type of *S. punctata*. This latter name should therefore be restored to this plant, and *S. davurica* Willd. relegated to synonymy as a '*nomen abortivum*'. *S. punctata* L., like *S. aestivalis* Fisch. & Mey., is now known to be widely distributed in Siberia. The identity of *S. punctata* L. and *S. davurica* Willd. is suggested by Fischer and Meyer (l.c. supra).

The identification of *S. punctata* L. by Haworth with the Irish plant allied to *S. umbrosa* was doubtless due to the superficial similarity of the foliage, and possibly in part to the citation in synonymy from Morison.

#### SAXIFRAGA UMBROSA L.

This species was first described in the second edition of Sp. Plant. p. 574 (1762), as follows:—

'14. *S. umbrosa*. *S. foliis obovatis subretusis cartilagineo-crenatis, caule nudo paniculato.*

*S. foliis cuneiformibus retusis radicalibus sinuato-serratis margine acutis, caule paniculato.* Hort. Ups. 108.

*Geum folio subrotundo minore, pistillo floris rubro.* Magn. Hort. 38, t. 88. Mill. ic. 141, f. 2.

*Hab. in montibus apud Cantabros.*

*Affinis nimium S. Geo; folia basi minime cordata, crenis angulatis; petiolis ciliato-villosis. Flores inferi.'*

The diagnosis in this case is an emendation of that in Hort. Ups., the first synonym, which is founded entirely on Magn. Hort. 88, t. 88. According to Hort. Ups. the plant is known 'in Alpibus Cantabrigicis, Rhaeticis, Pyrenaeis'. As with *S. hirsuta* so here Magnol's account cited by Linnaeus is a succinct

one from which the plant can be determined with sufficient accuracy. It is stated to develop rosettes of spreading subrotund leaves, thick, glabrous, shining, dark green, and narrowed below into a short, broad, villous-edged petiole; and the inflorescence is a panicle of white flowers, marked with red and yellow spots. The plant is said to have been found by Tournefort in the Cantabrian Mountains, and the accompanying figure, supplied by him, depicts a Saxifrage of this group, with oval foliage, resembling the *S. umbrosa* of the Pyrenees. The last synonym, quoted by Linnaeus from Miller's 'Figures of Plants' (i, t. 141, f. 2), is *Geum folio subrotundo majori, pistillo floris rubro* Tourn. (*Sedum montanum serratum guttato flore* Park.). Parkinson's figure agrees generally with the same Pyrenean *S. umbrosa*, but Miller's plate shows a slightly different form, probably drawn from the present-day 'London Pride' of gardens.

The Linnean Herbarium contains no specimen named *S. umbrosa* by Linnaeus; but pinned to the preceding sheets is one marked '13', that has a plant (without flowers) whose foliage resembles that of the Irish form with nearly glabrous petioles. On the back of this sheet is marked, in Linnaeus's hand, 'Hispania, 311. Loeff.'

In the absence of a Linnean type-specimen the identification of *S. umbrosa* L. depends solely on the original account in Sp. Plant. ed. 2, of which Magnol's description and figure form the main basis. There is little doubt but that Magnol had in view the Pyrenean form which has generally been accepted as the typical species.

#### MODERN TAXONOMY OF THE GROUP.

As some confusion may easily arise in discussing these plants through Linnaeus's practical transposition of the names *S. Geum* and *S. hirsuta*, the former appellation will be tentatively used for the more or less reniform-leaved plant to which it is commonly attached, while *S. hirsuta* will be taken in the usual sense to indicate the form considered intermediate between *S. Geum* and *S. umbrosa*.

The three species were well described and figured in 1795 by Lapeyrouse (Figures Fl. Pyrénées, pp. 44 &c.), who remarks of *S. hirsuta*: 'J'ai sur cette espèce des doutes que la culture n'a pas dissipés. Son nom spécifique conviendrait mieux à la suivante [*S. Geum*], de laquelle elle se rapproche bien moins que de l'*umbrosa*, quoiqu'en dise Linnaeus'. The figure (t. 23) differs from the Linnean specimen in that the foliar crenatures are fewer, coarser, and less rounded and inbricate. The flowers of *S. Geum* are stated by Lapeyrouse to be white and unspotted—probably a constant specific character,—and in this respect they do not agree with Magnol's plant, on which Linnaeus's name is founded.

In 1799 Sir J. E. Smith ('English Botany', no. 663) produced his account of *S. umbrosa*, taken from the form discovered in 1792 in Heseldon Gill, Yorkshire. This was followed in 1806 by *S. Geum* (E.B. 1561), which had been



found near Dingle in 1804 by J. T. Mackay, and in 1811 by *S. hirsuta* (E.B. 2322), based on Irish specimens cultivated at Dublin. The last-named plant does not match the Linnean original, having subrotund, coarsely dentate foliage, somewhat as in Lapeyrouse's plate.

Meanwhile a new species, *S. spathularis*, had been published with a full description in 1804 in Brotero's 'Flora Lusitanica', ii, p. 172. This is a Portuguese plant akin to *S. umbrosa*, differing chiefly in its subrotund, spathulate and dentate leaves. Brotero's name seems to have been consistently overlooked by most later authors, but it is identified with *S. umbrosa* by Seringe in DC. Prodr. iv, p. 42 (1830) and in Engler's Monograph of the genus (1872).

The group was constituted a new genus *Robertsonia* in 1812 by A. H. Haworth (Syn. Pl. Succ. App. pp. 322 sq.) and several new species established. These were *R. serrata*, an Irish plant compared with *S. punctata* L.; *R. polita*, a Scottish form, with reniform, sharply toothed leaves, also contrasted with *S. punctata*: *R. sphaeroidea*, of unknown origin, allied to *S. hirsuta*; and *R. crenata* (origin unknown) and *R. dentata* (from Scotland), both near *S. Geum*, but with spotted flowers. Nine years later Haworth re-arranged these plants (Saxifr. Enum. pp. 53 sq.), and we get (1) *R. Geum*, with  $\alpha$ . *Geum*,  $\beta$ . *dentata* (now said to be Irish),  $\gamma$ . *crenata*,  $\delta$ . *polita* (given as Irish), and  $\epsilon$ . *gracilis* (a garden form near *polita*); (2) *R. hirsuta*, with  $\alpha$ . *obliqua* (*S. hirsuta* L.),  $\beta$ . *atrovirens* and  $\gamma$ . *laetevirens* (garden forms),  $\delta$ . *hispida* (a fresh Irish plant with suborbicular, hispid foliage), and  $\epsilon$ . *sphaeroidea*; (3) *R. punctata* L. (a Siberian species), with  $\beta$ . *serrata* (Irish); and (4) *R. umbrosa*,  $\alpha$ . *longipes* (*S. umbrosa* L.) and  $\beta$ . *brevipes* (E.B. 663).

David Don's Monograph of *Saxifragaceae* was published in Trans. Linn. Soc. vol. xiii, in 1822, and here Haworth's species are excluded. Don admits (1) *S. Geum*, with vars.  $\beta$  and  $\gamma$ , both with glabrous leaves and the latter with large, spotted petals; (2) *S. hirsuta*, said to have pilose foliage, with var.  $\beta$ —*foliis glabris*; and (3) *S. umbrosa*, with  $\beta$ . *punctata* (*S. punctata* L.), having subrotund, deeply cut leaves, and  $\gamma$ . *serratifolia*—*foliis oblongo-ovatis, incisoserratis*. Don gives Siberia as a habitat for *S. Geum* in addition to the Pyrenees, Switzerland, and Ireland; *S. hirsuta* and *S. umbrosa* are said to grow in the Pyrenees and Ireland, while their varieties are Irish only.

About this period the different forms recently described seem to have been extensively distributed as garden plants. There are specimens in Herb. Mus. Brit., dated 1835, from Herb. Schleicher, of *R. polita*, *R. punctata*, *R. gracilis*, and others. And Reichenbach (Icon. Botan. pls. dcxxi-dcxxxviii (1829)) figured no less than seven species from cultivated examples. These were *S. hirsuta* L., *S. punctata* L. (*R. crenata* Haw.), *S. serratifolia* Mackay (*R. serrata* Haw.), *S. elegans* Mackay (*R. dentata* Haw.), *S. polita* (Haw.), and *S. Geum* L., with a new species, *S. modesta* Reichb., with small, long-petioled foliage and unspotted flowers. The figure of *S. hirsuta* shows coarsely, acutely crenate leaves, and recalls Magnol. t. 87 rather than the Linnean diagnosis and specimen (i.e. of *S. Geum*).

An elaborate account of these plants was published in 1831 in Supplement II to Sternberg's 'Saxifragarum Revisio'. *S. Geum* (p. 4) is divided into four varieties :— $\alpha$ . *Lapeyrousii*, with hirsute, broadly crenate foliage,  $\beta$ . *Linnaei*, with hirsute, obtusely dentate foliage,  $\gamma$ . *Haworthii* (*R. dentata* Haw., *S. modesta* Reichb.), with hirsute,  $\pm$ acutely dentate foliage, and  $\delta$ . *Donii* (*R. polita* and *R. gracilis* Haw., *S. elegans* Reichb.), with glabrate,  $\pm$ acutely dentate foliage. *S. hirsuta* (p. 5) has five varieties :— $\alpha$ . *Linnaei*, with glabrous, broadly crenate leaves,  $\beta$ . *Haworthii* (*R. sphaeroidea* Haw.), with glabrous, obtusely dentate foliage,  $\gamma$ . *Donii* (Irish), with hirsute,  $\pm$ acutely dentate leaves with the base cordate to cuneate,  $\delta$ . *Smithii* (E.B. 2322), with glabrous, acutely dentate leaves, and  $\epsilon$ . *hybrida*, a garden product with subrotund, acutely dentate, cuneate-based foliage. The common Irish plant described by Haworth as *R. serrata* is maintained as a third species, *S. serrata*, which is divided into  $\alpha$ . *Haworthii*, with obtusely dentate leaves,  $\beta$ . *Reichenbachii*, with acutely dentate leaves,  $\gamma$ . *Breana*, with more acutely dentate leaves,  $\delta$ . *Morisonii*, with ovoid rather than subrotund foliage, and  $\epsilon$ . *trichopoda*, with oval leaves and very hirsute petioles. All of the varieties are Irish. *S. umbrosa* (p. 6) has four varieties :— $\alpha$ . *Tournefortii*, with broadly oval leaves and short petioles,  $\beta$ . *Linnaei*, with oval, crenate leaves and longer petioles,  $\gamma$ . *Smithii*, with more dentate foliage, and  $\delta$ . *cordata*, with broader, acutely dentate leaves. This species is stated to grow in the Pyrenees and the mountains of Scotland and Ireland.

Mackay, who early in the century had collected specimens in Ireland which were described by Don and others, gives his account of the group in 'Flora Hibernica', p. 64 (1836). Of *S. Geum* he has four varieties. One of these, *R. dentata* Haw., which is stated to be the commonest form, is said to have glabrous foliage like *R. polita* Haw. A new species from Torc Mountain appears as *S. elegans*, which apparently had been previously introduced by Don as a variety of *S. Geum*. *S. hirsuta* is described from the Gap of Dunloe and is said to agree with the specimen in the Linnean Herbarium. *S. umbrosa*, of which E.B. 663 is cited as a synonym, is given as plentiful in woods in Kerry and Cork ; a var.  $\beta$  (*R. punctata* Haw.) is shown for Carnual, Mayo, and Connemara ; and var.  $\gamma$  (*S. serratifolia* Don) for the Gap of Dunloe.

In 1844 *S. umbrosa* var. *serratifolia* Don was figured in 'English Botany', Supplement 2891, the account being written by Babington, who divides the species into  $\alpha$ . *crenata* (E.B. 663),  $\beta$ . *crenato-serrata*, which seems to be the 'London Pride' of gardens,  $\gamma$ . *punctata* Don, and  $\delta$ . *serratifolia* Don. The plate, showing 'the most extreme deviation from the Pyrenean type', depicts foliage with very long, acute teeth, and subrotund rather than oblong-ovate in outline. The succeeding year E.B.S. 2892 (*S. elegans*) and 2893 (*S. Geum* var. *serrata*) were published with descriptions also by Babington. There are further notes on these plants by Babington in Trans. Bot. Soc. Edinburgh, ii (1846), containing *inter alia*, a figure of a leaf of *S. hirsuta* (pl. ix, f. 11), which closely resembles the Linnean specimen (of *S. Geum*). It is stated to have been drawn from a Pyrenean example in Herb. Dr. Leo, of Metz.

Syme, in the third edition of 'English Botany' (vol. iv, pp. 68-70 (1865)) has *S. Geum*,  $\alpha$ . *crenata*,  $\beta$ . *serrata*, ? $\gamma$ . *elegans*; *S. hirsuta*; and *S. umbrosa*,  $\alpha$ . *genuina*,  $\beta$ . *punctata*,  $\gamma$ . *serratifolia*. Of the last-named species, var.  $\alpha$  is stated to occur in Great Britain, and vars.  $\beta$  and  $\gamma$  to be equally widely distributed in Ireland. Syme's arrangement has been frequently followed in subsequent British works.

A noteworthy feature of Engler's 'Monographie der Gattung *Saxifraga*' (1872) is the identification of *S. spathularis* Brot., which is not mentioned in British text-books, with *S. umbrosa* L. There is no allusion to *S. spathularis* in Willkomm and Lange's 'Flora Hispanica', iii, p. 174 (1874), but at the end of the account of *S. umbrosa* (p. 125) an observation is inserted 'Planta gallicica et asturica foliorum serratura grossa ad *S. serratifoliam* Mackay accedit'.

Rouy and Camus (Fl. France, vii, p. 35 (1901)) describe a Pyrenean *S. hirsuta* with glabrate, crenate foliage, that seems akin to the Linnean specimen of *S. Geum* and distinct from the forms hitherto distinguished from Irish material. A hybrid  $\times S. hirsutoformis$  Rouy & Cam. (*S. hirsuta*  $\times$  *umbrosa*), stated to have been found in various Pyrenean localities with the parents, is also included. *S. Geum* has two varieties,  $\beta$ . *minor* and  $\gamma$ . *elegans* (*S. elegans* Mackay). It is noted that the latter is not a hybrid, but whether it is identical with Mackay's Irish form may be doubted.

A new variety *acutidens* of *S. hirsuta* was described in 1912 by E. S. Marshall in Journ. Bot. 1. p. 198, separable from the Linnean plant chiefly by its serrate instead of crenate foliage.

There is a comprehensive account of these plants in Engler and Irmscher's *Saxifrageae* in 'Pflanzenreich', iv, 117, i (1916), which is largely based on the method of Sternberg. *S. Geum* is divided into two subspecies, *Eu-Geum* and *hirsuta*, and *S. serrata* is reduced to a variety of *S. umbrosa*. Under subspecies *Eu-Geum* (p. 168) four varieties are admitted:—*Lapeyrousii* (Sternb.), *dentata* (Haw.), *argute-serrata*, an Irish plant, and *modesta* Reichb. The subspecies *hirsuta* (p. 172) has two varieties with hirsute foliage, *parcepilosa* (*R. atrovirens* and *laetevirens* Haw.) and *Donii* (Sternb.); and five with glabrous foliage, *sphaeroidea* (Haw.), *apiculato-crenata*, a form cultivated in Scotland and Yorkshire, *polita* (Haw.), *elegans* (Mackay), and *gracilis* (Haw.). *S. umbrosa* (p. 174) shows three varieties, *typica*, *Smithii* Sternb. and *serratifolia* Don, the last with the forms *Morisonii*, *Breana*, *Reichenbachii*, and *Haworthii*, adopted from Sternberg. *S. spathularis* Brot. is identified with f. *Morisonii*. The collaborateurs include one hybrid, the Pyrenean  $\times S. hirsutoformis$ , described by Rouy and Camus.

In 1916 also appeared Dr. Scully's 'Flora of County Kerry', which deals intensively with the forms of south-west Ireland. Scully regards *S. Geum* and *S. umbrosa* as two true species, and considers all the other forms distinguished, including *S. hirsuta*, as hybrids between them. *S. elegans*, *S. polita*, and *S. gracilis* fall within this category. In forming this opinion Scully does not rely entirely on his observations in the field, but also on experiments carried out at Trinity College, Dublin, where forms matching

some of the wild intermediates were produced by crossing *S. Geum* and *S. umbrosa*, and conversely, by self-pollinating wild Irish *S. hirsuta*, varying seedlings were obtained, among which some closely resembled *S. Geum* and others *S. umbrosa*. Scully's view is supported by Dr. Praeger. The common Irish plant generally regarded as *S. umbrosa* var. *punctata* Don appears to be treated as the typical species by Scully.

#### CONCLUSIONS.

It is curious that, while in the sixteenth century *Saxifraga rotundifolia* L. was so familiar as a garden plant that it was endowed with a popular name 'Prattling Parnell' by Gerard ('Herball', p. 645 (1597)), the forms of *S. umbrosa* and *S. Geum* were unknown. As already shown, a form of *S. umbrosa* was first described in Parkinson's 'Paradisus' (1629), and two forms, one of *umbrosa* and one of *Geum* affinity, were cultivated at Paris in 1665. A second *umbrosa*- and a second *Geum*-like plant were obtained by Tournefort in Spain and the Pyrenees, and the four forms were grown at Montpellier in 1697, when Magnol published his 'Hortus Regius Monspelienensis'. It appears from Boerhave (Pl. Lugd. p. 91 (1710)) that three of these Saxifrages were also cultivated at Leyden, and a reference to the Sloane Herbarium shows that different forms were grown at Hampton Court (Uvedale), the Chelsea Physick Garden (P. Miller), and in the Duchess of Bedford's garden. Early in the eighteenth century Irish forms too were to be found in cultivation.

Tournefort's *Geum folio subrotundo minori, pistillo floris rubro*, which is Linnaeus's *Saxifraga umbrosa*, is so well described by Magnol (l.c.) that it is unmistakably the Pyrenean form repeatedly collected in later times, as already noticed. The rosette of subrotund, thick leaves lying on the ground, with short, villous-edged petioles, and the panicles of white flowers with yellow and crimson spots and reddish capsules admit of no doubt respecting the plant's identity. Tournefort evidently regarded this plant as distinct from his *G. folio subrotundo majori, pistillo floris rubro*, which had been known since Parkinson's time and was extensively cultivated. No good early description of this latter plant can be traced, but Miller (l.c.), who figures it under Tournefort's name, with Parkinson's as a synonym, and adds the English 'None-so-pretty' and 'London Pride', remarks that it has long been cultivated in English gardens. He adds truly that it propagates fast by offsets, but his further remark that it grows naturally on a mountain in Kerry in Ireland is more doubtful. The plate is only partially satisfactory. The general aspect of the plant is correct for the present-day 'London Pride', as are also the rather long petioles and the relatively large, finely speckled flowers; but the leaf-margins are poorly shown, and the ciliation of the petioles is omitted. There is little doubt, however, but that the figure was drawn from 'London Pride'. It is noteworthy that no capsules are portrayed in the plate. In my experience 'London Pride', unlike all other forms that I have cultivated, is completely sterile, and this has been observed by other gardeners. Nearly all the *exsiccatæ*

of this form that I have examined are likewise without capsules, the only certain exceptions being a cultivated specimen at Kew, received from Mackay and said to have come from Glengariff, and a recent gathering from Orkney (Johnston, no. 3638). This absence of fruit might well be attributed to hybridity, but sterility does not seem to characterise the numerous crosses in this group that certainly may be found in south-west Ireland, and it seems more probable that it has been induced in this case by continual vegetative propagation in gardens extending over a very long period. The Sloane Herbarium contains examples recognisable as 'London Pride' from Plukenet (H.S. 83/181) as well as from Miller (H.S. 294/75), and in Smith's herbarium there is a specimen 'Hort. Hb. Banks, 1786'. The same form was also collected by W. Andrews in 1844 at Dingle and two other stations in Kerry, and more recently at Dingle by E. S. Marshall, who noted it as 'type *umbrosa*, very rare in Ireland'. But it is by no means clear that it is a native plant in Kerry, and, seeing that it had been cultivated in Britain for nearly two centuries before it was found there, it is very possible that it is an escape, as in county Wicklow and elsewhere in Ireland, as well as in Great Britain and on the continent. The Glengariff and Orkney specimens mentioned above agree with typical *S. umbrosa* in the form of their styles and capsules, and, judging from this and the plant's general features, it seems reasonable to follow Babington in treating 'London Pride' as a taxonomic variety of that species whose origin is uncertain.

The native Irish 'London Pride', discovered in 1697, was figured by Petiver in 1715, and described under Parkinson's name (with Tournefort in synonymy) in 1727 by Threlkeld. In Hort. Cliff (p. 167), under '*S. foliis cordato-ovalibus crenatis emarginatis, caule nudo, δ. Sanicula montana rotundifolia minor hispanica* Ray Hist. 1047', Linnaeus writes 'Crescit in Alpibus Helvetiae et montibus Hiberniae,' and thus notes the existence of a plant of this group in Ireland. But there is no reference to an Irish locality in Sp. Plant. The specimen in Herb. Linn., unnamed and without flowers but resembling the common Irish form, came from Spain.

Haworth first separated this Irish plant from *S. umbrosa* in Syn. Plant. Succ. App. p. 322 (1812) as *Robertsonia serrata*, which he afterwards (Saxifr. Enum. p. 55 (1821)) converted to a variety *serrata* of *R. punctata* (*S. punctata* L.). Don (Mon. Saxifr. p. 352) makes this plant a variety *punctata* of *S. umbrosa*, and adds a var. *serratifolia* for another Irish form with oblong-ovate instead of subrotund leaves. Sternberg (Revis. Saxifr. Suppl. ii, p. 5 (1831)) maintained Haworth's species as *S. serrata*, with numerous varieties, all from Ireland.

All of these writers overlooked the Portuguese *S. spathularis* Brotero, which had been published in 1804 (Fl. Lusit. ii, p. 172). Brotero's account is in considerable detail. *S. spathularis* is characterised by spatulate, subrotund, dentate leaves, borne on petioles twice their length and ciliate only at the base; and by a pubescent scape of white spotted flowers. There is material of this plant in Herb. Mus. Brit. (Welwitsch, Fl. Lusit. no. 914) and at Kew

(Univ. Coimbra, no. 417, Gerez), and this may readily be seen to be identical with the common Irish form named *R. serrata* or *S. serrata* by Haworth and Sternberg. Its points of difference from *S. umbrosa* are important and seemingly constant. The leaves, even at maturity, are ascending, subrotund or oval (var. *serratifolia* Don), acute and dentate with relatively few teeth, while in *S. umbrosa* they are spreading, subrotund-oblong or cuneiform, obtuse or truncate, and crenate with numerous lobules. The petioles of *S. spathularis* are proportionately much longer than in the other, and ciliate only about the base instead of throughout. The scape of *S. spathularis* is glandular-pilose rather than glandular-pubescent; and its capsules are greenish and shortly cylindric, with short divaricate styles much inflated below, somewhat as in the forms of *S. Geum*. The capsules of *S. umbrosa* are tinted with red, cylindric-conic, with longer divergent but not divaricate styles. These differences, especially those of the fruit, taken in conjunction with the plants' distinct geographical areas, seem to warrant the retention of *S. spathularis* Brot. as a separate species.

Turning to the *S. Geum* forms it now becomes necessary to use the correct instead of the commonly accepted nomenclature. It has been shown that the original *S. Geum* of Sp. Plant., of which there is a type-specimen in Herb. Linn., is an entirely different plant from that which has been associated with the diagnosis of *S. Geum*, supported by Morison's figure, in the second edition of the same work. The original *S. Geum* is said to grow 'in alpinis helveticis, pyrenaicis', but Linnaeus's specimen was a cultivated example from Hort. Cliff. Lapeyrouse (l.c.) remarks that this species is more akin to *S. umbrosa* than to *S. hirsuta* L. (*S. Geum* auct.), and expresses doubt as to its status, although he gives a number of Pyrenean habitats. His figure (as *S. hirsuta*) portrays a plant sufficiently different from Linnaeus's; it is less like *S. umbrosa*, its leaves being subrotund and subtruncate below, with fewer, broader, angular teeth or crenatures. The figure of E.B. 2322 (as *S. hirsuta*) is not very different. Willkomm and Lange (l.c.) do not admit a third species for Spain distinct from *S. umbrosa* and *S. hirsuta*. Rouy and Camus (l.c.) apparently intend to describe (as *S. hirsuta*) the form seen by Lapeyrouse, but their account recalls largely the features of the true *S. Geum*.

Most of the material seen in herbaria that can be accurately identified with the Linnean type-specimen of *S. Geum* was obtained from cultivated or presumably naturalised plants. Such are Reichb. no. 2448 (Steyr, Upper Austria); Pichler, Gastein, Salzburg; Jacquet, Forêts des Vosges; Joad, Vallée d'Aoste, 1882; and Ehrhart, Pl. Select. Hortul. no. 93 (the last three in Herb. Kew.). Two wild specimens at Kew, however, also closely match this form. They are both from the Pyrenees (Spruce, 'Eaux Bonnes', 1845, and Hb. Hooker, rochers élevés, Bonjean, 1867). Other material in Herb. Kew. indicates that varying hybrids between *S. hirsuta* L. and *S. umbrosa* L. are to be found in those mountains. There is a further example in Sir J. E. Smith's herbarium, annotated '*S. hirsuta* E. B. Sent from the Gap of Dunloe,

Killarney, by J. T. Mackay in 1804', which is almost exactly like the Linnean type of *S. Geum*, as was noted by Mackay (l.c.), and is very different from any other Irish Saxifrage that has been examined. It does not look like a hybrid between *S. hirsuta* L. (*S. Geum* auct.) and any form of *S. spathularis*, but it may have arisen from the former species crossed with 'London Pride', which is known to grow at Dingle. At the same time it is possible that it was not a true native at Killarney. The form is not known to have been subsequently collected.

From the available evidence it would appear that *S. Geum* was described by Linnaeus from cultivated specimens of a plant of unknown origin, which has become widely naturalised. A few wild Pyrenean specimens in herbaria agree approximately with the description and the type, and, as the form and cutting of its foliage, and also its floral characters, are intermediate between *S. umbrosa* of the Pyrenees and *S. hirsuta* L., it is likely that *S. Geum* is a hybrid originally obtained in that region where the parent species grow in company. In these circumstances it appears advisable to retain the binominal name, under which it may be treated as a pure species or a hybrid.

A number of other varying Irish intermediate forms have similarly been referred to *S. Geum* L. (*S. hirsuta* auct.). Most of these show deeply and sharply cut, glabrate foliage, and sometimes glabrate petioles, from which it may be inferred that they are hybrids of which *S. spathularis*, rather than *S. umbrosa*, is one parent, as would be expected in Ireland. The plant distinguished by Marshall (l.c.) as *S. hirsuta* var. *acutidens*, which occurs in more than one locality, more closely resembles Mackay's Gap of Dunloe plant and the Linnean type of *S. Geum*, and may be regarded as a good variety of *S. Geum*. It is possibly a cross with *S. spathularis* var. *serratifolia* (Don).

The remaining Linnean species, *S. hirsuta*, originally named *S. rotundifolia* through inadvertence, is founded on a single synonym from Magnol's Hort. Monsp., which is repeated in the second edition of Sp. Plant., although the specific diagnosis is materially altered there. In this case there is no type-specimen. Magnol's plant is accurately described (l.c.) and fairly figured under the name of *Geum folio circinato acute crenato, pistillo floris rubro*. It is said to produce round, crenate leaves, hirsute above and glabrous below, on long, pilose petioles, and panicles of white, red-spotted flowers, succeeded by red capsules. The plate shows cordate, crenate-dentate leaves about as broad as long. Such a plant must be typical *S. hirsuta* L. Magnol's plant is described from a new species in Tournefort's 'Elémens de Botanique' (l.c.), where it immediately follows *G. folio circinato, pistillo floris pallido* T., which had previously been distinguished as *Sanicula montana crenata flore pallido* H. R. Paris. Both plants were known not only to Magnol and Tournefort, but to Boerhave (Pl. Lugd. p. 91 (1710)), and the latter was brought into cultivation at Paris at least as early as 1665. No detailed description of this plant can be found, but Tournefort by his nomenclature indicates how the two forms may be distinguished. The earlier differs from Magnol's plant

by its leaves being crenate but not acutely so, and its capsules pale or greenish instead of red. This points to the form of *S. Geum* auct. with entirely hirsute, obtusely crenate foliage, and white unspotted flowers, which are succeeded by capsules that do not redden.

Most authors have described *S. hirsuta* L. (*S. Geum* auct.) as having spotted flowers, or flowers spotted or unspotted, but Lapeyrouse (l.c.), who knew it well in the Pyrenees, states definitely 'pétales blancs immaculés'. As this species certainly hybridises freely in south-west Ireland with *S. spathularis*, it may be expected that in the Pyrenees it acts similarly in company with *S. umbrosa*, and both of these species having red-spotted flowers, it is likely that the petals of a proportion of any hybrids produced would likewise be spotted. And these hybrids, re-crossing with *S. hirsuta*, might well produce plants with spotted flowers that otherwise were scarcely separable morphologically from this species. After seeing *S. Geum* auct. *in situ* both in the Pyrenees and in Kerry, I am forced to the conclusion that Lapeyrouse's conception of the plant is right, and that the pure species is a slender plant with light green, hirsute, obtusely crenate leaves, and slender panicles of white flowers without any red spots, in which green and not red capsules are developed. This appears to be the plant originally named *Sanicula montana crenata umbilico pallido*. If this is so, the typical Linnean *S. hirsuta* is of hybrid origin, and being a native of the Pyrenees, it can only be crossed with *S. umbrosa*. How far it has become a fixed form, having the facies of a true species, is a matter for investigation. In south-west Ireland *S. hirsuta* has crossed very freely with *S. spathularis*, and a general difference between the Irish and the Pyrenean forms with spotted flowers may be observed in the foliage, the Irish plants, on an average, having distinctly more dentate leaves due to the influence of *S. spathularis*. Hence the variety *dentata* (Haw.), to which few Pyrenean examples can be referred, is prevalent in Ireland.

The pure white-flowering species was treated by Sternberg (l.c. p. 4) as a var. *Lapeyrousii* of *S. hirsuta* (*S. Geum* auct.), and this treatment was followed by Engler and Irmscher (l.c. p. 168). If Magnol's plant, the basis of the Linnean species, is a hybrid, the var. *Lapeyrousii*, as a pure species, cannot be retained under it. It is therefore proposed to separate it as a distinct species, *S. lactiflora*, no specific name other than *S. hirsuta* or *S. Geum* having hitherto been applied to it. As some uncertainty may be held to attach to the status of the spotted-flowered *S. hirsuta*, it seems at least convenient to retain it, like *S. Geum* L., as a provisional taxonomic species.

Of the other Irish forms that have been distinguished, *Robertsonia polita* Haw. is doubtless a hybrid, *S. hirsuta* × *spathularis*, with rotund, sharply dentate, glabrous foliage; *S. elegans* Mackay, Fl. Hibern. p. 64, is a second form of the same parentage, notable for the extremely short petioles of its somewhat similar leaves—it is well represented in Herb. Kew. Another distinct form is that figured as *S. hirsuta* in E.B. 2322 (1811). This was drawn from an Irish specimen cultivated at Dublin, and, as already indicated, is, curiously,



almost identical with the *S. hirsuta* of Lapeyrouse (Fig. Fl. Pyr. t. 23). It is notable for its glabrous, subrotund leaves, subtruncate but not cordate below, and coarsely dentate with broad, angular teeth and feebly developed cartilaginous margins. These named forms cover only a few of the numerous combinations of characters due to hybridity that may be found in south-west Ireland and probably also in the Pyrenees. It is not known how far any of them have become stable and constant in a wild habitat.

It has already been shown that *S. punctata* L., which was confused with *S. spathularis* by Haworth and D. Don, and with *S. aestivalis* Fisch. & Mey. by Sternberg and subsequent continental authors, is really identical with the Siberian *S. davurica* Willd.

The British forms, with their synonymy, may be shown as follows :—

SAXIFRAGA L., Sect. ROBERTSONIA (Haw.) Engler.

\* Leaves numerous, ± cuneate below, narrowed to broad, flat petioles.

1. SAXIFRAGA UMBROSA L. Sp. Pl. ed. 2, 574 (1762) ; Lapeyrouse, Fig. Fl. Pyr. 44 (1795) ; Smith, E. B. 663 (1799) ; Don, Mon. Saxifr. in Trans. Linn. Soc. xiii, 352 (1822), excl. vars. ; Sternberg, Rev. Saxifr. Suppl. ii, 6 (1831), excl. var.  $\delta$  ; Babington, E. B. Suppl. 2891 (1844), as var. *crenata* ; Syme, E. B. ed. 3, iv, 70 (1865), excl. vars.  $\beta$  and  $\gamma$  ; Willkomm & Lange, Fl. Hisp. iii, 125 (1874) ; Rouy & Camus, Fl. Fr. vii, 34 (1901) ; Engler & Irmscher, Saxifr. in Pflanzenreich, iv, 117, i, 174 (1916), excl. var.  $\gamma$  ; *Robertsonia umbrosa* Haw. Saxifr. Enum. 55 (1821).

*Geum folio subrotundo minori, pistillo floris rubro.* Tourn. Fl. Bot. i, 218 (1694) ; Magnol, Hort. Monsp. 88 (1697).

*Icones.* Magnol, l.c. t. 88 ; Lapey. l.c. t. 22 ; E. B. 663 ; Reichb. Icon. Botan. f. 841 ; Sternb. l.c. t. xviii, ff. 7–10 ; Engl. & Irmsch. l.c. f. 45 f.

*Exsicc.* Bordère, no. 12103, Héas, Htes-Pyrénées ; Billot, no. 768 ; Endress, Eauxbonnes, Pyr.-Occid., 1831, in Hb. Mus. Brit. ; Bourgeau, Pyr.-Espagnoles, no. 440 ; René de Parquet, Castaneze, Aragon, 1862, in Hb. Mus. Brit. ; F. Schultz, Hb. Norm. no. 664 ; Borrer, Glutton Gill, Yorks, in Hb. Mus. Brit. ; Fl. Exsicc. Austro-Hungarica, no. 615, Ternberg, Austria Sup<sup>r</sup>. [copiose et certe spontanea-Zimmerer].

Leaves of flowering shoots rosulate, subrotund-oval to oblong-cuneate (of the turions shorter and broader), spreading at maturity, deep green, thick and ± coriaceous, obscurely veined, glabrous, obtusely and often subimbricately crenate (number of crenatures 4–10 on each side), subtruncate with the flattened terminal lobe shorter and broader than the others, broadly cartilaginous-edged, and cuneate or rather abruptly narrowed below to a broad, flat petiole with margins densely ciliate throughout, and often much shorter than the lamina, but sometimes as long or even rather longer. Scape slender, suffused with red, glandular-pubescent especially above. Corolla 7·5–9 mm. in diameter ;

the narrow, white petals each with a yellow basal spot and a few crimson specks above; ovary of opening flower very small. Capsule cylindric-conic, reddish, with ascending-divergent styles.

*β. crenato-serrata* Bab. in E. B. 2891 (1844). London Pride.

*Sedum montanum serratum guttato flore.* Park. Theatr. Bot. 738 (1640); *Geum folio subrotundo majori, pistillo floris rubro.* Tourn. El. Bot. i, 218 (1694); Magnol, Hort. Monsp. 87 (1697).

*Icon.* Miller, Fig. Plant. i, t. 141, f. 2.

*Exsicc.* Berveiller, Ballon de Grubwiller, Alsace, 1892; Chelsea Garden, nos. 3285 & 1126 (1744), 2837 (1778); Andrews, Dingle, 1844; Marshall, Culbone, 1907; Frankland, Thorp Arch; Ley, Ashwood Dale, Derbyshire: all in Hb. Mus. Brit. Johnston, no. 3638; Metcalfe, Buxton, 1822; Mackay, Woods of Glengariff, 1805 (cult.); Andrews, Couminsh and Graun Kad, Kerry, 1844: all in Hb. Kew.

Leaves larger and less spreading than in the type, subacute with generally more numerous (up to 12 on each side) and angular crenatures; petiole usually as long as the lamina. Scape taller, many-flowered, with glandular hairs fewer and longer below. Corolla about 9 mm. in diameter, with broader petals more finely speckled with crimson; ovary larger in the opening flower. Capsule rarely developed. Otherwise like the type.

*Hab.* Cantabrian Mts. and probably elsewhere in Northern Spain; Western, Central, and Eastern Pyrenees, both on the Spanish and French side; Ternberg, Upper Austria, probably naturalised only; Heseldon and Linn Gills, Yorkshire, perhaps native, but possibly relicts of the small-flowered form of the species mentioned by Ray.

Var. *β.* In Kerry, but probably naturalised there as in other parts of Ireland; naturalised in various localities in England and Scotland, and also in Alsace.

2. *S. SPATHULARIS* Brotero, Fl. Lusit. ii, 172 (1804); *Robertsonia serrata* Haw. Syn. Pl. Succ. App. 322 (1812); *R. punctata* var. *serrata* Haw. Saxifr. Enum. 55 (1821); *S. umbrosa* var. *punctata* Don, Mon. Saxifr. in Trans. Linn. Soc. xiii, 352 (1822); Bab. E. B. Suppl. 2891 (1844); Syme, E. B. ed. 3, iv, 70 (1865); *S. serrata* Sternb. Rev. Saxifr. Suppl. ii, 5 (1831); *S. umbrosa* var. *β.* Mackay, Fl. Hibern. 64 (1836); *S. umbrosa* Scully, Fl. Kerry, 103 (1916); *S. umbrosa* var. *serratifolia* Engl. & Irmsch. Saxifr. in Pflanzenreich, iv, 117, i, 174 (1916).

*Sedum montanum serratum guttato flore.* Threlkeld, Syn. Stirp. Hibern. (1727), non aliorum.

*Icones.* Sternb. l.c. t. xi (as *S. hibernica*), and t. xviii, ff. 12, 13, 15, 16, & 17; E. B. S. 2891, as *S. umbrosa* var. *serratifolia*; Reichb. Icon. Botan. f. 845 (as *S. serratifolia*); Engl. & Irmsch. l.c. f. 45 g.

*Exsicc.* Welwitsch, Fl. Lusit. no. 914; Fernandes, S. da Estrella, 1920; Murray, S. de Gerez, 1887, as *S. umbrosa*; Durieu, Pl. Sel. Hispano-Lusit. no. 330, as *S. umbrosa*; Bourgeau, Pl. d'Espagne, 1864, no. 2645, as *S. umbrosa*; Wilmott & Lacaita, Iter Hisp. 1927, Puerto de Ponton, Leon; Carroll, Carntuol, Kerry, 1853, as *S. umbrosa*; A. B. Lambert, Croagh Patrick, Mayo, as *S. umbrosa*; Praeger, Cashel, 1894, and Clare Island, 1910, as *S. umbrosa*; Marshall, no. 4030, as *S. umbrosa*: all in Hb. Mus. Brit. Univ. Coimbra, Gerez, no. 417, in Hb. Kew.

Leaves of flowering shoots loosely rosulate, spatulate or subrotund, ascending and not lying flat at maturity, deep green, thick and  $\pm$  coriaceous with obscure veins, glabrous, coarsely dentate,  $\pm$  acute, with the terminal tooth as long as those adjoining, the teeth not numerous (4-7 on each side), triangular and  $\pm$  acute, or sometimes elongate and sharply pointed, distinctly cartilaginous-edged, cuneate or abruptly narrowed below to a broad flat petiole much longer than the lamina and subciliate with a few pilose hairs usually near the base. Scape rather robust, generally glandular-pilose throughout. Corolla 9-11 mm. in diameter; the narrow white petals with 1-3 yellow basal spots and numerous crimson marks above; ovary of opening flower about twice as large as in *S. umbrosa*. Capsule shortly cylindric, scarcely narrowed above, greenish in colour, with short divaricate styles inflated below.

*$\beta$ . serratifolia*, comb. nov.

*S. umbrosa* var. *serratifolia* Don, l.c.; Mackay, l.c. (excl. syn.); Syme, l.c.

*Exsicc.* Andrews, Dingle, Kerry, 1844, in Hb. Mus. Brit., as *S. umbrosa* var. *serratifolia*; Pugsley, no. 519, Wicklow.

Leaves normally lighter green, oval or oblong, more rarely subrotund, acute, and serrate with more numerous (6-9 on each side), sharply pointed teeth. Scape usually very glandular with relatively compact inflorescence. Otherwise like the type.

*Hab.* Serra da Estrella and Serra da Gerez, Portugal; Galicia, Leon, and Asturias, N. Spain; S. & W. Ireland.

Var.  *$\beta$* . In Ireland only; Kerry, with the specific type, and Lugnaquilla, Co. Wicklow.

\*\* Leaves fewer, cordate or truncate below, with slender petioles.

3. *S. GEUM* L. Sp. Pl. 401 (1753) (excl. syn.), et ejusdem herb.; Syst. Nat. ed. 10, 1026 (1759); *S. hirsuta* L. Sp. Pl. ed. 2, 574 (1762) (excl. syn.); Lapey. Fig. Fl. Pyr. 45 (1795)?; Mackay, Fl. Hibern. 64 (1836); Rouy & Camus, Fl. Fr. vii, 35 (1901)?; Scully, Fl. Kerry, 99 (1916), ex parte; *Robertsonia sphaeroidea* Haw. Syn. Pl. Succ. App. 322 (1812); *R. hirsuta* vars. *obliqua* and *sphaeroidea*, Haw. Saxifr. Enum. 54 (1821); *S. hirsuta*  $\alpha$ . *Linnaei* Sternb. Rev. Saxifr. Suppl. ii, 5 (1831); *S. Geum* subsp. *hirsuta* var. *sphaeroidea* Engl. & Irmsch. Saxifr. in Pflanzenreich, iv, 117, i, 172 (1916).

*Icon. Engl. & Irmsch. l.c. f. 44 c.*

*Exsicc.* Spruce, Eaux Bonnes, 1845, as *S. hirsuta*; Hb. Hooker, Bonjean, 1867, as *S. hirsuta*; Jacquet, Forêts des Vosges, as *S. umbrosa*; Joad, Vallée d'Aoste, 1882, as *S. hirsuta*; Ehrh. Pl. Sel. Hortul. no. 93 (1793), as *S. hirsuta*: all in Hb. Kew. Reichb. no. 2448, Steyr, Upper Austria, as *S. hirsuta*; Pichler, Gastein, Salzburg, 1864, as *S. umbrosa*; Berne Bot. Garden, ex Hb. Roemer, in Hb. Mus. Brit., as *S. umbrosa*; Mackay, Gap of Dunloe, 1804, in Hb. Smith, as *S. hirsuta*.

Leaves of flowering shoots scarcely rosulate, broadly oval, ascending, deep green, rather thick and coriaceous, obscurely veined, glabrous, somewhat finely and subimbricately crenaté (9–13 rounded or flattened crenatures on each side), retuse through the apical crenature being shorter than those adjacent, broadly cartilaginous-edged, subcordate or truncate below, with a narrow, slightly flattened, pilose petiole at least twice as long as the lamina. Scape glandular-pubescent. Corolla about 9 mm. in diameter; petals with a yellow basal spot and a few crimson marks above. Capsule shortly cylindric, ± tinted with red, with short styles apparently a little less divaricate than in *S. spathularis*.

*β. acutidens*, comb. nov.

*S. hirsuta* var. *acutidens* E. S. Marshall in Journ. Bot. I. 198 (1912).

*Exsicc.* Marshall, no. 3647, Connor Hill; Scully, Slieve Mish and Torc Mt., 1908, in Hb. Mus. Brit., as *S. hirsuta*.

Leaves subtruncate at the base, with fine, subacute teeth rather than rounded crenatures, and more narrowly cartilaginous margins; petiole about three times as long as the lamina. Otherwise like the type.

*Hab.* Eaux Bonnes (and Bonjean?), Basses-Pyrénées; Gap of Dunloe, Kerry, Ireland; Vosges Mts.; Valley of Aosta, Piedmont; Gastein, Salzburg; Steyr, Upper Austria; probably naturalised in all except the Pyrenean stations.

Var. *β*. In several localities in Co. Kerry, Ireland, of uncertain status.

4. *S. HIRSUTA* L. Sp. Pl. 401 (1753), emend. Syst. Nat. ed. 10, 1026 (1759); Seringe in DC. Prodr. iv, 42 (1830); Gren. & Godr. Fl. Fr. i, 639 (1848); Willkomm & Lange, Fl. Hisp. iii, 125 (1874); Coste, Fl. Fr. ii, 132 (1903); *S. Geum* L. Sp. Pl. ed. 2, 574 (1762), excl. syn. C. B. P. & Morison (non fig.); Sternb. Rev. Saxifr. Suppl. ii, 4 (1831), as var. *Linnaei*; Rouy & Camus, Fl. Fr. vii, 36 (1901); Scully, Fl. Kerry, 96 (1916), ex parte; Engl. & Irmsch. Saxifr. in Pflanzenreich, iv, 117, i, 168, as subsp. *Eu-Geum* var. *Lapeyrousii* f. *maculata* and f. *crenata*; *Robertsonia crenata* Haw. Syn. Pl. Succ. App. 322 (1812); *R. Geum* var. *crenata* Haw. Saxifr. Enum. 53 (1821).

*Geum folio circinato acute crenato, pistillo floris rubro.* Tourn. El. Bot. i, 218 (1694); Magnol, Hort. Monsp. 87 (1697).

*Icones.* Magnol, l.c. t. 87; Morison, Hist. iii, f. 12, t. 9, f. 12; Sternb. l.c. t. xviii, f. 1 a 3; Reichb. Icon. Botan. f. 849.

*Exsicc.* Bordère, no. 12061, Gèdres; Willkomm, Iter Hisp. secund. no. 1, Yrun; F. Schultz, Hb. Norm. no. 665; Endress, Pas de Roland, Pyr.-Occid. 1831; Chelsea Garden, no. 2834 (1778); Dawson Turner, Killarney; Ibbotson, Collinton Woods, Edinburgh, 1841: all as *S. Geum*; Billot, no. 559: all in Hb. Mus. Brit.

Plant of slenderer habit than the three preceding species. Leaves of flowering shoots subrosulate, rotundate, generally rather longer than broad, but occasionally broader than long, ascending, bright green and often purplish below, less thick and coriaceous than in *S. umbrosa* or *S. Geum* but obscurely nerved, commonly hirsute on both surfaces with coarse, pilose hairs but sometimes glabrate below, typically dentate-crenate with subacute, generally coarse crenatures (8-13 on each side), obtuse or even retuse owing to the flattened apical crenature,  $\pm$  narrowly cartilaginous-edged and usually deeply cordate, with a narrow, scarcely flattened, strongly pilose petiole twice or thrice as long as the lamina. Scape very slender, finely glandular-pubescent, sometimes with longer hairs below. Corolla about 9 mm. in diameter; the narrow white petals with a yellow basal spot and red specks above. Capsule shortly cylindric, greenish  $\pm$  tinted with red, with short divaricate styles inflated below.

*$\beta$ . dentata*, comb. nov.

*Robertsonia dentata* Haw. Syn. Pl. Succ. App. 323 (1812); *R. Geum* var. *dentata* Haw. Saxifr. Enum. 53 (1821); *S. Geum* var. *Haworthii* Sternb. l.c. 4; *S. Geum* Bab. E. B. S. 2893 (1845); *S. Geum* var. *serrata* Syme E. B. ed. 3, iv. 68 (1865); *S. Geum* subsp. *Eu-Geum* var. *dentata* Engl. & Irmsch. l.c. 168.

*Icones.* E. B. S. 2893; Engl. & Irmsch. l.c. f. 43 g.

*Exsicc.* Andrews, Connor Hill, 1844; Ridley, Torc Mt., 1883 (partim): both in Hb. Mus. Brit. as *S. Geum*.

Leaves dentate with  $\pm$  acute teeth, hirsute on both sides. Otherwise like the type.

*Hab.* Western and Central Pyrenees, probably also in northern Spain; Co. Kerry and Co. Cork, Ireland.

*Var.  $\beta$ .* Chiefly in south-west Ireland.

5. *S. LACTIFLORA*, sp. nov. *S. Geum* Lapey. Fig. Fl. Pyr. 46 (1795), non Linn.; Smith, E. B. 1561 (1806); Syme, E. B. ed. 3, iv, 68 (1865), as var. *crenata*; Scully, Fl. Kerry, 96 (1916), ex parte; *S. Geum* var. *Lapeyrousii* Sternb. Rev. Saxifr. Suppl. ii, 4 (1831); *S. Geum* var.  $\delta$ , Mackay, Fl. Hibern. 64 (1836); *S. Geum* subsp. *Eu-Geum* var. *Lapeyrousii* f. *albiflora* Engl. & Irmsch. Saxifr. in Pflanzenreich, iv, 117, i, 168 (1916); *Robertsonia Geum* var.  $\alpha$ , Haw. Saxifr. Enum. 53 (1821).

*Sanicula montana crenata umbilico pallido*. Jonoquet, Hort. Reg. 161 (1665)? *Geum folio circinato, pistillo floris pallido*. Tourn. El. Bot. i, 218 (1694); Magnol, Hort. Monsp. 87 (1697)?

*Icones*. Lapey. l.c. t. 24; E. B. 1561; Sternb. l.c. t. xviii, ff. 2, 4, 5, 6; Engl. & Irmsch. l.c. f. 43, a-f.

*Exsicc.* Soc. Dauph. no. 5398; Sennen, Pl. d'Espagne, no. 1673; Losa, Cubella, Sobron, Spain; Wilmott, St. Jean, Pied du Port, Basses-Pyrénées; Marshall, no. 3639, Cloghane: all as *S. Geum*; Bourgeau, Pl. d'Espagne, no. 2644, as *S. hirsuta*: all in Hb. Mus. Brit.; Pugsley, no. 520, Bigorre, Hautes-Pyrénées (type); Pugsley, no. 521, Mt. Brandon.

In habit and general characters closely resembling *S. hirsuta* L., but with lighter green foliage hirsute on both surfaces; leaf-cutting variable, crenatures (6-13 on each side) sometimes few and broad, sometimes narrower and more numerous, the apical often shorter and broader than those adjacent. In some Irish forms the leaves are more dentate. Corolla with narrow, white petals showing a  $\pm$  distinct yellow basal blotch, but without any red or crimson markings; anthers yellow. Capsule always green, with short divergent styles much inflated below.

I have marked as the specific type a plant which I myself collected along the banks of a stream in the hilly meadows near Bigorre, Hautes-Pyrénées, where it was quite uniform and far from any habitat of *S. umbrosa*.

*Hab.* Asturias and probably elsewhere in northern Spain; Western and Central Pyrenees; Co. Kerry and Co. Cork, Ireland.

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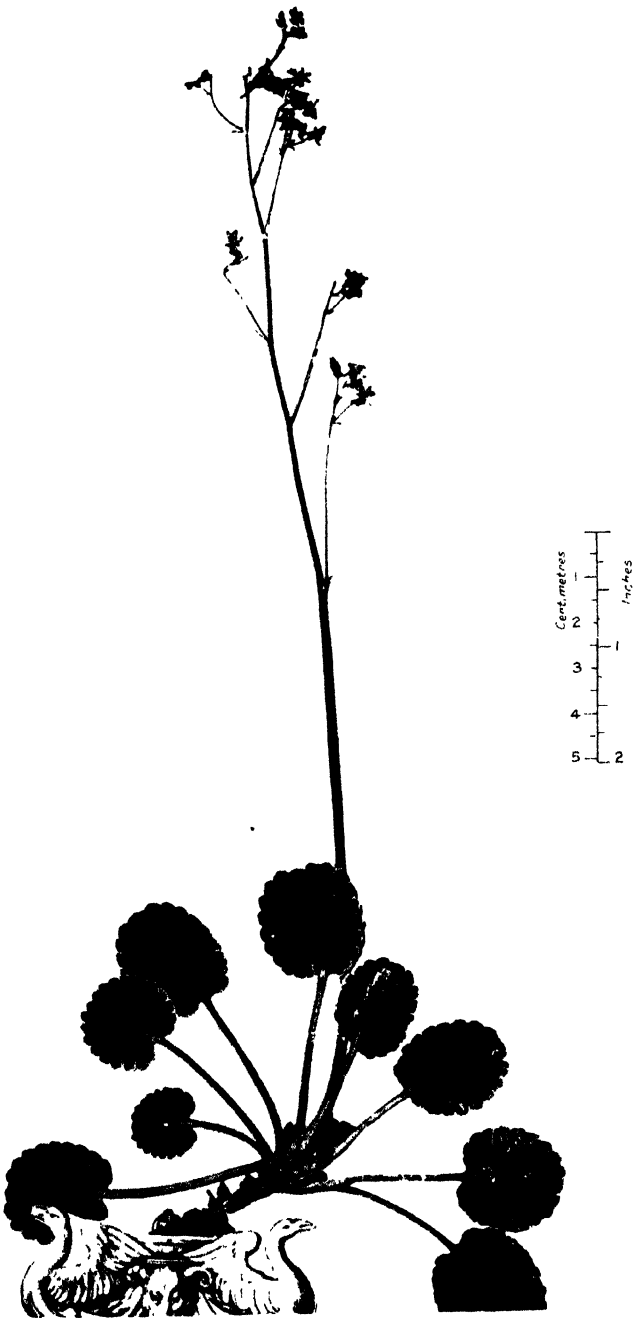
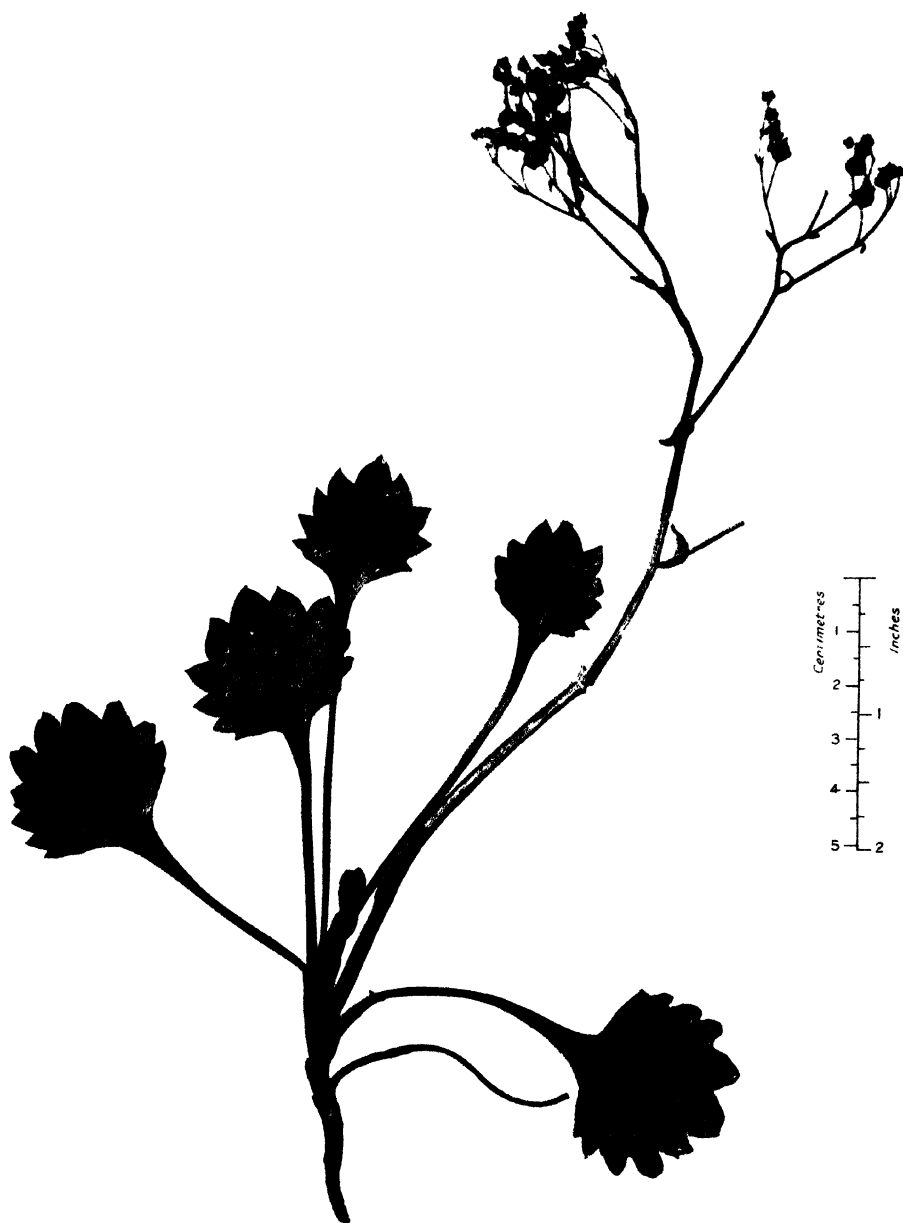


Fig. 1. Saxifraga geum 154

SAXIFRAGA GEUM







*punctata* 13

John Bar Sole & Thacker 1841 mod.

SAXIFRAGA PUNCTATA



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## EXPLANATION OF THE PLATES.

## PLATE 6.

*Saxifraga Geum*. The specimen in the Linnean Herbarium—  
 about three-fifths natural size.

## PLATE 7.

*Saxifraga punctata*. The specimen in the Linnean Herbarium—  
 about three-fourths natural size.



On rhythmic development and radial organisation in the flower. By EDITH R. SAUNDERS, F.L.S., sometime Fellow of Newnham College, Cambridge.

(With 33 Text-figures)

[Read 9 May 1935]

# 1. CONSIDERATIONS OF GENERAL PRINCIPLES.

It is scarcely necessary to emphasise the point that the whole ground-plan of the flower—in other words, the number and arrangement of the several members composing it—often cannot be determined by mere inspection, even if the examination is repeated at successive stages in development. Such an examination will tell us that the number of floral members present is *not less than* the number of individual structures that we see partly or completely disjoined, but in many cases this method fails to disclose whether or not the number is *higher than this minimum*. I need only cite in illustration of this difficulty the calyx in *Cypripedium*, *Ulex*, and *Scutellaria*, the corolla in *Calceolaria* and many Composites, the single perianth in *Aristolochia*, the androecium in *Soldanella*, the gynoeceium in a *Primula*.

It is clear that we need some other criterion which will suffice when the outward appearance leads to uncertainty. Such a criterion is afforded by the vascular scheme, for the vascular ground-plan and the floral ground-plan are directly bound up together, hence if we are not able to decide the above question by the one method we may be able easily to do so by the other. For the two ground-plans are expressions of the same morphological scheme in different terms. The one, as much as the other, is the outcome of certain inherent rhythmic processes which bring about the orderly and symmetrical disposition of the component units. These rhythmic developments are common knowledge. In the first place there is in the floral, as in the vegetative, shoot the primary rhythm which takes effect in the length direction, bringing about the regular alternation of nodes and internodes. A secondary rhythmic process manifesting its effects at the nodes leads to the formation of separate individual floral members and to their regular disposition.

When we proceed to consider this latter rhythmic process in further detail it is found convenient to deal separately with the acyclic and the cyclic type. On the more elongated axis of the acyclic flower the 'beats' in the rhythmic process, for so we may regard the successive exertion points of the floral members, lie on a regular uninterrupted spiral\*. The floral members follow

\* Though a change of rhythm may occur when there is a sudden marked change in the exertion width of successive members, as e.g. at the point of transition from corolla to androecium.

one another at successively higher levels on *approximately equidistant radii*. In such flowers each member is, as a rule, exerted separately\*, hence the floral ground-plan is readily ascertainable on inspection. We shall not, therefore, concern ourselves further here with this class, but can confine our attention to cyclic forms, in which, owing to fusions, or, as we should perhaps say, to non-disjunction or non-segmentation, outward form is often no longer a wholly safe guide. In these types the shortening of the floral axis reduces the time and the space available for the development of the series of floral members. The necessary saving in time and economising of space has been effected by breaking up the simple even rhythm characterising the acyclic type and the production of a double rhythm expressed in the succession of the 'beats', not at equal intervals throughout, but in recurrent series. We can, then, view the cyclic type as arising from the acyclic simply through a change in the rhythm of development—through the speeding-up, at regular intervals and for definite periods, of the formation of floral members. As a result, the turns of the spiral traced in each of these periods become so flattened that the members lying on them appear to form a whorl. But the spiral trend has not disappeared. Though more or less obscured during the development of the whorl it becomes manifest as each new whorl is initiated. After each period of speeding-up there is a period of reaction. The lateral interval between the last member of one whorl and the first of the succeeding whorl is not identical with that between the successive members of an individual whorl. It may be larger or smaller, the outcome in either case being the same. The first member, and consequently all the members of the new whorl, are in this way brought on to the set of radii alternating with that of the preceding whorl †.

Now, although this arrangement of alternating whorls is so general that we should expect it to rest on a principle of universal application, we are nevertheless familiar with a large number of instances in which it appears to break down, often in circumstances which do not suggest that an additional whorl was originally present and in the course of evolution has become suppressed.

There is, for example, the very large class of isomerous six-whorled types ‡ in which the androecium is obdiplostemonous and the ovary loculi lie on the radii of the petals, whereas strict alternation should bring them in line with the sepals. There are also some five-whorled types having only one whorl of stamens, in which this whorl is superposed upon the preceding perianth whorl. Furthermore, in certain genera, which include some species with the full number of whorls and others in which an intermediate whorl has undoubtedly been suppressed, the radial position of the later whorls is the same in both groups. These facts are also common knowledge, but a satisfactory explanation has hitherto been lacking. When, however, it is realised that underlying the floral ground-plan is a strictly related, if not identical, vascular

\* Some gynoecea excepted.

† Unless these relations are disturbed by fusion, partial or complete (see later).

‡ Types, that is, with two perianth, two stamen, and two carpel whorls.

ground-plan, and that it is primarily in the vascular ground-plan that the inherent rhythm of organisation on alternate sets of radii is expressed, then the various kinds of exceptions to the general rule of alternating whorls of members become intelligible. Furthermore, it becomes possible to define the conditions which give rise to these exceptions and therefore to predict when they will occur, and, finally, to bring them all into line with the general rule.

It is not a little astonishing that, although the vascular ground-plan was successfully employed as a means of elucidating the orchidaceous floral ground-plan rather more than seventy years ago, but little use has since been made of this method for investigating the problems presented in floral morphology.

An examination of the floral scheme in a large number of genera of the hypogynous class\* shows that for our present purpose such types can conveniently be divided into two groups. In the one group the central vascular cylinder changes but little in diameter in the region of the flower base. This being so, the strands which become the midribs of the members of the successive whorls, from the moment at which they become delimited, all follow a centrifugal course, running directly outwards from the central cylinder through the axis ground tissue to the shortly-to-be exerted members which they serve. In the other group the central cylinder expands considerably at the flower base. The process of organisation of the strands for the inner whorls proceeds centripetally. In types in which development follows this latter course the appearance seen in transverse section usually shows a much less regular arrangement than when the sets of strands for the different whorls turn directly outwards, and in the initial stages of the organisation process anastomoses may obscure any indication of a definite pattern in relation to the two sets of construction radii. The appearance then is more comparable with that characteristic of nodes in some vegetative axes. But as the process of delimitation is completed the bundles for each whorl in due course take up their proper radial positions before passing into the members for which they are destined. The point of importance in the present connection is that, *typically, in both modes of development a single strand is formed on the radius of each member which, traversing the ground tissue of the axis, enters and becomes the midrib of that member.*

We thus find, as we might expect, that the vascular ground-plan rests upon the same principle of radial symmetry as the floral ground-plan. The two are identical† except when fusion (non-disjunction) of bundles takes place. Where this correspondence appears not to hold investigation shows that the discrepancy does not indicate a real divergence but is the result of some secondary

\* The reason for the selection of hypogynous types is obvious. The various fusions which have taken place in the vascular system of syngonous forms are more readily analysed if the principles underlying the less condensed scheme of hypogynous types is clearly grasped.

† Or evidently they have been so in some ancestral form, although in its descendants to-day parts of the original vascular system are lacking through degeneration.

complication due to various causes, such e.g. as fusion of superposed bundles : vascular degeneration resulting in the disappearance of the basal (connecting) region, or even of the whole of some or of all the bundles, on one set of radii : precocious branching of the bundles while still traversing the ground tissue of the axis so that a pair of laterals (or occasionally more than one), as well as the midrib bundle, enters the exerted member ; or, in sepals with commissural laterals, organisation of these laterals at an even earlier stage.

In types in which the first of the above-mentioned conditions is present, that is when the midrib bundles for two superposed members emerge from the central cylinder as a single trunk cord, which is resolved at a later point into its components, the total number of separate bundles leaving the central cylinder of the axis will obviously be fewer than that of the members which they serve. Fusion of this nature is common between the bundles of the perianth and androecium, occurring in types in which the stamens are exerted directly from the axis as well as in those in which they are epipetalous.

In types in which gradual degeneration of the midrib bundles is ultimately followed by their complete disappearance, although the corresponding floral members still retain their outward form, a condition not infrequently found in the two-whorled androecium, the total number of bundles turning out from the central cylinder will again not accord with the number of floral members. But in many of these cases evidence is available showing that this discrepancy is of secondary origin. Thus, although the bundles have disappeared from a staminal whorl in some genera of the Geraniaceae (*Erodium*) and Amaran-taceae (*Alternanthera*) they are present in other related genera (e.g. *Geranium* and *Gomphrena*). Or the bundles may have only partially disappeared as in some *Polyanthus* \* individuals, in which although the basal part of the main bundle has been lost, the disconnected branch system still persists.

In types coming under the third head mentioned above, in which three (or more) separate bundles enter the exerted member, the mode of origin of the additional strands—by lateral branching, at an unusually early stage, of the out-turning midrib bundle—shows that here too there is no real lack of conformity between the floral and the vascular ground-plans. Instances of such premature branching of the midrib bundles below the exertion level but outside the central cylinder may be seen in the bundles for the sepals of *Rhododendron racemosum* and *Hypericum aegypticum*, in those for the petals of some Cistaceae and of *Zebrina pendula* among Monocotyledons, in those for

\* In earlier references to the interpretation of the vascular scheme of the Primulaceae I have cited species of *Androsace* and *Cortusa* besides *Polyanthus* as showing partial degeneration of the antesepalous stamen bundles. I therefore take the opportunity to state that I have since been able to confirm this observation in *Polyanthus* individuals and in *Androsace*, but that I have not met with it again in *Cortusa*. It is therefore possible that the *Cortusa* specimen originally examined was altogether exceptional in this respect and that vascular degeneration of this nature is not usual in this genus (see (12), p. 264, footnote 1, and (14), p. 137).



the sterile carpels of species of *Hypericum* and *Oxalis*. So far as I am aware, branching of the bundle is never found either before or after exsertion in the *individual* stamen of the typical form characteristic of cyclic types if it is fully functional, but is quite frequent when such members become sterile, as is seen, e.g., in the petaloid staminodes of *Soldanella*, *Clavija*, *Jacquinia*, *Labatia*, and even in the incompletely fertile stamens of *Salvia*.

## 2. CONSIDERATION OF APPARENT EXCEPTIONS TO THE PRINCIPLES OUTLINED ABOVE.

### (i) *Obdiplostemony and antepetalous loculi in isomerous six-whorled flowers.*

In those types in which the midrib bundles for the successive whorls all arise independently, and in which there is no differential development of the disk or other unequal development of the axis as between the two sets of radii, there can, I think, be no doubt that obdiplostemony is the direct result of the different degree of radial extension attained by the sterile and the fertile carpel whorls, respectively. This connection is well exemplified by some isomerous types in the Caryophyllaceae and by comparable types in the alliances Geraniales and Ericales. In *Agrostemma* and in specimens of *Stellaria aquatica* Scop. with an isomerous gynoeceum the loculi are antepetalous—nevertheless, the androeceum is not appreciably obdiplostemonous, for the two whorls of carpels have the same radial dimension, a transverse section of the ovary showing an even circular outline with the midrib bundles of both whorls lying on the same circle; hence the bundles for both stamen whorls also lie on a common circle. On the other hand, in six-whorled isomerous types in the Geraniales, with the exception of the Linaceae, the radial dimension of the two carpel whorls is very different and obdiplostemony is correspondingly well-marked. In Ericaceae and Pirolaceae, where the difference in these radial dimensions is not so considerable, the obdiplostemonous condition is less pronounced.

On the above view it becomes possible to refer all cases of true obdiplostemony in types coming under the above head\* to one common cause. It may be noted, however, that in some species not coming into this category a condition unconnected with gynoeceum configuration not infrequently occurs which will presumably have the effect of at least facilitating, if not of causing, the obdiplostemonous arrangement. In the species referred to the antepetalous stamen bundles do not arise separately but are carried out conjoined with the petal midrib bundles, and in this way are brought to a position further from the centre than that reached by the independently arising antesepalous stamen bundles.

Now although we can explain simply and fully the hitch in alternation occurring in obdiplostemonous types between the second and third whorls by

\* i.e. types in which the midrib bundles for all the whorls arise independently.

viewing it as a secondary induced effect produced by the configuration of the carpels, it still remains to account for the primary cause lying behind this effect, viz. the hitch in alternation occurring between the fourth (inner staminal) and fifth (outer carpel) whorls which brings the sterile carpels into line with the petals, whereas, if alternation held good throughout, they would lie on the sepal radii. Three classes of facts point the way to an explanation, as will appear from what follows:—

(i) Types in which the vascular ground-plan is identical with the floral ground-plan, i.e. types in which the midrib bundles for the members of all whorls leave the central cylinder separately, are relatively few. In such isomerous six-whorled types, unless some special counteracting condition or structural feature outbalances the natural result, *the outer carpels (and hence the loculi), contrary to the general rule of alternating whorls, appear to be invariably antepetalous*. In the majority of such six-whorled species fusion of the bundles of some superposed whorls for a longer or shorter distance is a regular feature. That is to say, the midrib bundles of (usually) two superposed members leave the central cylinder *as a single trunk cord*, which later undergoes dissociation into its components. It may, perhaps, be well at this point to make clear that by the above phraseology it is not intended to imply that *two sets of organised elements* are presumed to lie side by side in one strand and later to separate, but rather that two *developmental potentialities* co-exist in the one strand and that later each reaches separate expression. It is, of course, possible to look at the above relationship from the opposite standpoint and to describe the midrib bundle of the inner of two such whorls as fitting on at its lower end to that of the member of the outer whorl upon which it is superposed. But it does not appear to me that anything is gained by viewing these relations in this reverse way\*, rather the contrary. But whether we trace the bundle systems in the one direction or the other is not of moment for our present purpose, for in whichever manner we visualise these relations we reach the same conclusion, viz. *that, in order to meet within a certain limit of time the difficulty created by restriction of space, the bulk of isomerous six-whorled types have adopted as an alternative to reduction in the number of members in the inner whorls the plan of the trunk cord*. It having become difficult when the full number of isomerous whorls is present for all the bundles to arise directly from (or fit directly on to) the central cylinder, some of the bundles have come to leave (or, if one prefers so to regard the process of development, to enter) the cylinder associated together.

The most usual cases of fusion of the kind indicated are between the antepetalous stamen bundles and those of the petals, or between both sets of stamen bundles and those of both perianth whorls, the former of these conditions being extremely common. *It appears that when such fusions occur the superposed whorls served by a single set of trunk cords behave from the point*

\* i.e. from above downwards instead of from below upwards,

of view of alternation as a single whorl. Thus when the antepetalous stamen bundles are carried out conjoined with the petal bundles, while the antesealous stamen bundles originate independently the outer carpels (and loculi) are antepetalous. Whereas, if the bundles of both stamen whorls issue from the central cylinder conjoined with the bundles of the perianth members these carpels are antesealous, although the number of whorls is identical in the two cases.

(ii) The obdiplostemonous condition, so far as I am aware, never occurs in Monocotyledons. Although an isomalous six-whorled ground-plan is characteristic of nearly all types in Liliaceae, Commelinaceae, Pontederiaceae, Juncaceae, Flagellariaceae, and Rapateaceae, yet in every case alternation of the whorls is maintained throughout. [I have elsewhere drawn attention to the fact that Seubert's floral diagram of *Rapatea paludosa*, which appears in Martius's 'Flora Brasiliensis' (16) and has been reproduced in later systematic works, in which the loculi are represented as antepetalous and in which, therefore, obdiplostemony is to be presumed, is incorrect. In the material which I examined the loculi were antesealous as in other isomalous Monocotyledons (see (15), pp. 657, 689).] *In no members of the above families so far examined do the bundles for either stamen whorl originate independently, while in every case, as on the present conception is therefore to be expected, the outer carpels and loculi are antesealous.*

(iii) In those isomalous six-whorled types in which the midrib bundles for all whorls originate independently, but in which the natural outcome of this ground-plan is outbalanced by some other structural feature, which has the effect of affording more space or more time for the expansion of the later whorls alternation of the whorls continues throughout. Thus in *Stachyurus praecox* Sieb. & Zucc. (see (15), p. 683, and figs. 132-139) the greater dimension of the stamen-bearing disk structure on the sepal radii inevitably brings about a diplostemonous condition, hence the outer carpels are antesealous. Again, where the presence of a gynophore or stipe allows carpel expansion to be delayed until a level is reached at which the restraint exerted by the outer whorls is removed, the outer carpels are again able to develop on the sepal radii as happens in various isomalous Caryophyllaceae.

The above facts and others which can be interpreted on the same lines lead to the following conclusions :—

1. That the fundamental principle of floral construction in existing cyclic forms is not solely, nor primarily, that of the alternation of successive whorls of *members* but of the alternation of successive whorls of *outgoing strands* destined to become midrib bundles of the floral members, either directly if the strand corresponds to a single bundle having a single developmental potentiality, or after resolution if the strand corresponds to a compound bundle or trunk cord with a twofold developmental potentiality.

2. That when the outgoing strands which become midrib bundles represent single bundles, i.e. have one developmental potentiality, floral ground-plan and vascular ground-plan will coincide,

3. That when the outgoing strands for six successive isomerous whorls all turn outwards independently and in such rapid succession that at the level at which those for the sterile carpels emerge the tissue of all the whorls is still continuous, a state of 'congestion' is set up after the emergence of the strands for the fourth (second staminal) whorl, with the result that when developmental activity is resumed to produce the fifth (outer carpel) whorl the growth impetus has shifted along the growth spiral to the alternate set of radii, so that the sterile carpel bundles issue on the petal radii and the loculi are antepetalous.

4. That in isomerous types, those in which such a state of 'block' is set up excepted, the principle of alternation is followed throughout in the *vascular* ground-plan. That when in such types the *floral* ground-plan departs from this fundamental rhythm the deviation appears to be of secondary origin, being brought about by the organisation of the midrib bundles of separate whorls at their point of origin as a single set of trunk cords.

5. That when the outgoing strands represent trunk cords, i.e. when each such strand furnishes a midrib to two superposed whorls, these two whorls will behave as a unit whorl in the scheme of alternation. Hence, although the successive whorls of *strands* alternate, a hitch may nevertheless occur in the regular alternation of the successive whorls of *members* which they supply.

6. That in the process of condensation, which gives rise to systems of trunk cords, lies the explanation of the fact that further reduction resulting in the complete suppression of a whorl can take place without involving the shifting of the next succeeding whorl from its proper set of radii to the alternate set. After trunk cords have left the central cylinder their subsequent behaviour, i.e. whether they continue as a single strand or become resolved into two, has no effect upon the radial position of either the next set of strands leaving the central cylinder or of the members for which they are destined.

We may now proceed to illustrate the above conclusions by reference to numerous hypogynous or perigynous isomerous types among both Dicotyledons and Monocotyledons.

As the explanatory abbreviations accompanying the figures are the same throughout, the complete list is given here in order to avoid repetition:—

<i>cl</i> , commissural laterals.	<i>rvtg</i> , residual vascular tissue for the
<i>d</i> , disk.	gynoecium.
<i>fc b</i> , fertile carpel bundle.	<i>S 1</i> , <i>S 2</i> , <i>S 3</i> , <i>S 4</i> , <i>S 5</i> , Sepal 1, &c.
<i>f c m</i> , fertile carpel midrib.	<i>sc m</i> , sterile carpel midrib.
$\frac{1}{2}$ <i>f c m</i> , fertile carpel midrib divided in	<i>s m</i> , sepal midrib.
half.	<i>st</i> , stamen bundle.
<i>l</i> , loculus.	<i>tc 1</i> , trunk cord 1 (+ <i>st</i> + <i>f c m</i> ).
<i>pl</i> , placental strand.	<i>tc 2</i> , trunk cord 2 ( $\pm$ <i>cl</i> + <i>p m</i> + <i>st</i> + <i>sc m</i> ).
<i>p m</i> , petal midrib.	<i>tl</i> , true lateral branches.
<i>r S 1</i> , <i>r S 2</i> , <i>r S 3</i> , <i>r S 4</i> , <i>r S 5</i> , radius of	<i>t pl</i> , twin placental strands of one
Sepal 1, &c.	carpel.

## DICOTYLEDONS.

It will be convenient to consider first some examples of the smaller class which, having two stamen whorls, nevertheless show no hitch in alternation at any point.

## CORIARIACEAE.

*CORIARIA MYRTIFOLIA* L. The bundles for the several whorls turn out independently. The petals are roughly triangular in cross section, fitting like wedges between the carpels. The apocarpous gynoecium is composed of a single whorl of valve carpels. The isomerous flower is, therefore,  $K\ 5\ C\ 5\ A\ 5+5\ G\ 5+0$ . Here, since only five whorls are present, the 'blocking effect' or 'state of congestion' which comes into play under similar conditions in the six-whorled flower is not set up. Consequently, in isomerous specimens the carpels (fifth whorl) alternate with the inner stamen (fourth) whorl, and ovaries and loculi are thus antesealous. The diplostemonous condition is particularly pronounced owing to the peculiar shape of the petals.

## RANUNCULACEAE.

*XANTHORRHIZA APIIFOLIA* L'Hér. The determining conditions are probably the same here as in *Coriaria*. The gynoecium is completely apocarpous and is composed in the isomerous flower of one or two isomerous whorls of valve carpels. Here, as in *Coriaria*, owing to the apocarpous condition, there is no 'blocking effect' even when, as in some specimens, two carpel whorls are present. Consequently in  $K\ 6\ C\ 6\ A\ 6+6\ G\ 6+6$  flowers, as well as in the much more usual  $K\ 6\ C\ 6\ A\ 6+6\ G\ 6+0$  type there is no superposition of the fifth whorl upon the fourth, the outer carpel whorl, in accordance with the principle of alternation, standing on the radii of the sepals.

## CEPHALOTACEAE.

*CEPHALOTUS FOLLICULARIS* Labill. This species, the only known representative of this small family, has an isomerous hexamerous flower with a single perianth, two whorls of stamens, and an apocarpous gynoecium. It has been generally held to be most nearly allied to Crassulaceae, differing outwardly from this family chiefly in having only one perianth whorl and in lacking hypocarpellary scales. It will be recalled that the perianth members show a central green region with a broad white strip on each side. This coloration, and the alternate position of the large outer stamens \*, led Baillon (1), pp. 335, 428, to ask whether

\* There is some confusion in the various accounts of this plant regarding the position of the two forms of stamens. Baillon (loc. cit) describes the larger stamens (filaments longer and stouter) as being alternate with the perianth members and they are so figured in the 'Botanical Magazine'. But in the text accompanying this plate the longer stamens are described as being opposite the perianth members (5), and the same statement is made by Diels (see (3)). In the material which I examined, the longer stamens were undoubtedly alternate with the perianth segments. It, therefore, appears that the contradiction in the 'Botanical Magazine' is due to an error in the text and that this may account for an incorrect description by later writers.

the perianth members should not rather be considered as petals than as sepals. Eichler (4), p. 436, on the other hand, held that a corolla had been suppressed and that the stamens were therefore to be considered obdiplostemonous. More recently Diels (3), p. 74, has expressed the view that there is no support for the suggestion that petals have disappeared, a supposition put forward on the ground that the flower would then be obdiplostemonous and that this relation, together with the isomery of the whorls, would bring the genus into closer accord with the Crassulaceae. Even so, as this latter writer points out, *Cephalotus* would still differ from Crassulaceae in not having the characteristic hypocarpellary scales, while in point of fact the flower is diplostemonous. To this criticism we may add the comment that neither Baillon's view nor that of Eichler is compatible with the facts as they stand, and, furthermore, that the assumptions made by both these authors are, in fact, wholly unnecessary. For an examination of the vascular scheme shows that the disposition of the whorls calls for no special explanation. At the flower base the vascular system is seen in cross section as a ring near the periphery of twelve cords. From the six on one set of radii arise the trunk cords which furnish the tepal midribs and the bundles for the antetepalous stamen whorl. From those on the alternate radii are derived the tepal commissural marginals, the bundles for the alternitepalous stamen whorl, and those for the (generally) six superposed ovaries. There are no petal bundles. In this latter fact we find the explanation of the marginal coloration of the tepals, for we have here a particularly beautiful example of petaloid colouring in the perianth members of an 'apetalous' flower when these members receive as commissural marginals the whole of that portion of the trunk cord on each petal radius which is external to the stamen bundle (see (13)). Each ovary receives a single bundle, the carpel midrib, from which the strand supplying the (usually) single ovule is detached below the loculus. The ovaries here, as in *Coriaria* and *Xanthorrhiza*, are thus monocarpellary. From the above account it will be obvious that with the floral ground-plan  $T\ 6\ A\ 6+6\ G\ 6+0$ , and with the vascular ground-plan described above, no state of congestion will be set up. Furthermore, it will be evident that the assumption that a corolla has become suppressed is not demanded in order to explain the diplostemonous arrangement, for the development of petals in an ordinarily apetalous flower in which the bundles of neither stamen whorl arise independently would not affect the inner-outer relations of the two stamen whorls. Where, as in the present instance, tepal marginals and alternitepalous stamen bundles are derived from a common vascular cord, this cord would in a  $K+C$  flower merely become resolved into three components instead of two, a petal bundle being formed between the sepal marginals to the outside and the stamen bundle to the inside.

#### ELATINACEAE.

ELATINE spp., BERGIA spp.  $K\ n\ C\ n\ A\ n+n\ G\ n+n$  and  $K\ n\ C\ n\ A\ n+0\ G\ n+n$ . In these genera the bundles for the stamens turn outwards conjoined

with the midrib bundles of the perianth members. Consequently, here again there is no blocking effect and normal alternation brings the bundles for the outer carpels in line with the sepals. In two species, *Elatine triandra* Schkuhr and *Bergia ammaniioides* Roxb., the antepetalous stamens are not developed. As the bundles for the stamens do not arise independently, but as components of trunk cords, and as these cords, which furnish the petal midribs, are still formed, the suppression of the antepetalous staminal whorl will not affect the radial position of the sterile carpels and the loculi, which remain antesepalous as in the six-whorled types. Thus the carpel position in these two species, which has hitherto constituted an anomaly, is shown to be in accord with the fundamental principle underlying radial position. Similar cases are to be met with in many other families (see later, pp. 306-308).

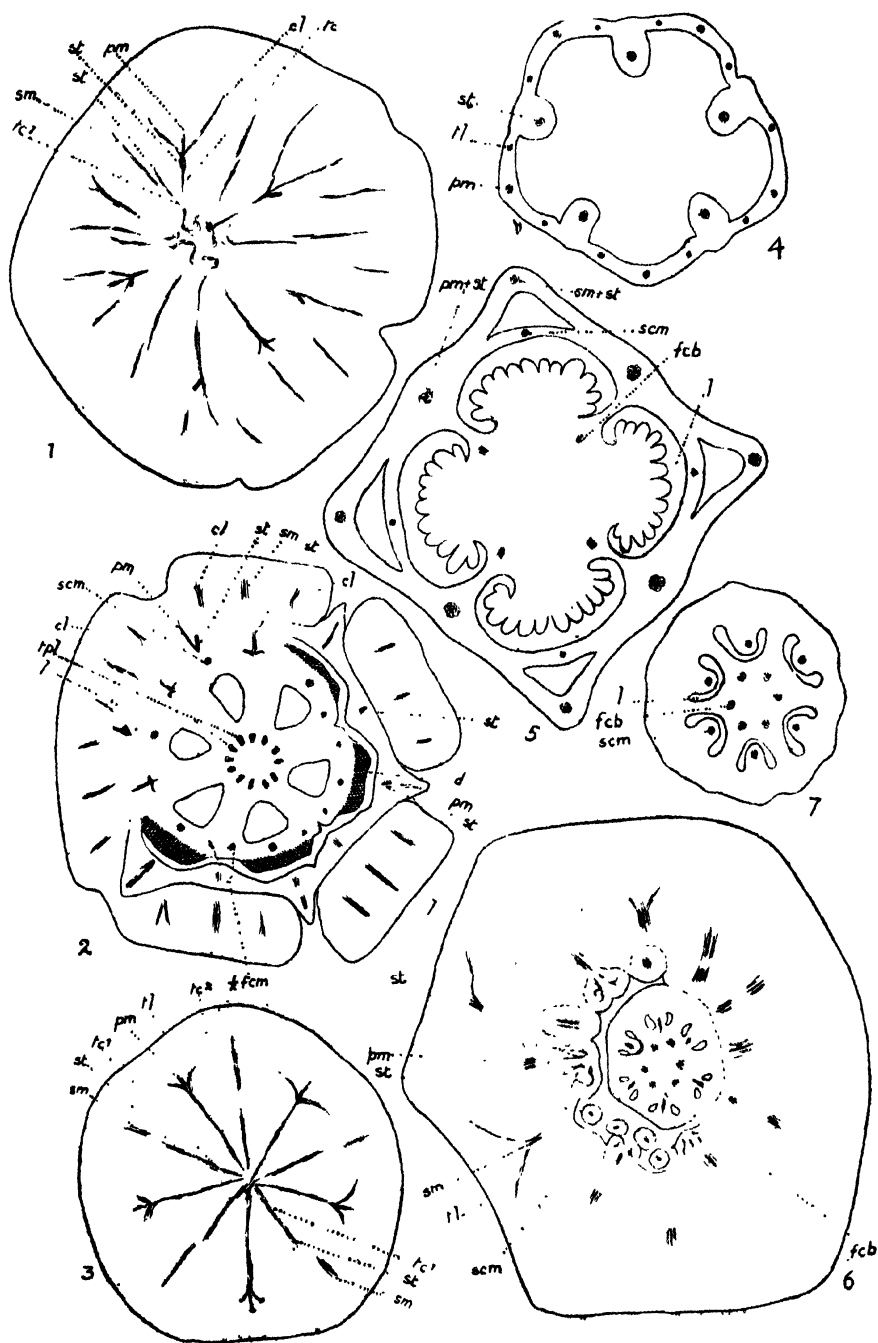
#### LYTHRACEAE. (Figs. 6, 7.)

Some six-whorled isomerous types with antesepalous loculi occur among the Lythraceae, though they constitute but a small minority of the whole family, in which great variety of ground-plan is to be found. The family is of special interest from the present point of view, since in not a few genera the principle of alternation would seem at first sight not to hold good.

Types with the ground-plan  $K n C n A n+n$  or  $n+n' G n+n$  are represented by species of *Lagerstroemia* and *Ammannia*.

Most species of *Lagerstroemia* have the formula  $K n C n A n+n' G n+n$ . Statements in the literature respecting the position of the loculi are contradictory. Eichler (4), p. 476, cites *Lagerstroemia* (together with *Ammannia*) as an isomerous type with antepetalous loculi, for which arrangement he adds that he can give no reason. But he would not, clearly, include in this generalisation *L. Flos-reginae* Retz., for his diagram of this species (loc. cit. p. 475, fig. 199 B) shows antesepalous loculi. He also represents this species as having antesepalous bundles of stamens, but no antepetalous members of the androecium, a ground-plan which, if a reality, would appear to be contrary to the general rule and to separate this species from the rest of the genus. Baillon (2), p. 455, on the other hand, gives 'ovary cells alternipetalous' as a characteristic of the genus. Koehne in 1898 described the fruit cells as antepetalous except in *L. indica*, in which they are *antesepalous*, (6), p. 4. But in 1903 this author reverses his earlier statement. Unaware, seemingly, of Eichler's general statement and of his diagram of *L. floribunda* Jack (loc. cit. p. 474, fig. 197 B), in which the loculi are represented as antepetalous, he cites *L. indica* L. as the solitary exception in which the loculi have constantly been stated to be *antepetalous*, (7), p. 12.

A microscopic examination of *L. indica* shows that the loculi, contrary to Eichler's account and to Koehne's later statement and in agreement with Baillon's generalisation, are formed on the radii of the sepals. The two whorls of carpels may be compared, as regards their configuration, with those of *Linum* (see (8), pp. 150, 151, and figs. 55-58, and (11), p. 112, Diagram 22).





## EXPLANATION OF FIGS. 1-7.

- 1-4. *Crassulaceae*. 1, 2, *Sedum alissimum* Poir. From a hexamerous flower. A slightly more advanced stage in development is shown on the right side of the drawings than on the left. 1. Flower base after the successive emergence on the one set of radii of the sepal midrib bundles and the trunk cords giving rise to the antesepalous stamen bundles and the midrib bundles of the fertile carpels; the latter bifurcate at once preparatory to the radial splitting, which results in pseudo-apocarpy. The single set of trunk cords formed on the alternate set of radii, which furnish the sepal commissural marginals, petal midribs, antepetalous stamen, and sterile carpel bundles, show various stages of resolution into their components. 2. The same at the level at which the calyx and corolla-stamen tube are partially exerted. Resolution of both sets of trunk cords is now complete on the right side of the drawing, but is still in process of taking place on the left. 3, 4, *Crassula multicava* Lem. Flower base showing a vascular ground-plan similar to that shown in 1 except that the scheme is pentamerous and that no sepal commissural marginals or antepetalous stamen bundles are developed. 4. The corolla-stamen tube; only the antesepalous stamen whorl is present. 5, *Melastomataceae*. *Centradenia floribunda* Planch. Flower base at the level at which the ovary is becoming disjoined from the flower (calyx-corolla-stamen) tube. The sterile carpels and loculi are antesepalous. The midribs of these carpels have already become detached from the one cord formed on these radii, but the residual portion of the cords is not yet resolved into sepal midrib and antesepalous stamen bundle. On the alternate radii are the trunk cords for petal midrib and antepetalous stamen bundle, also not yet resolved. 6, 7, *Lythraceae*. *Lagerstroemia indica* L. 6. Flower base as in 5. The sterile carpels are seen as complete septa halving the loculi in line with the sepals and single antesepalous stamens (or spaces which they occupied). On the alternate radii the petal and antepetalous stamen bundles in various stages of development. On the right one petal-stamen trunk cord still unresolved. On the neighbouring petal radius on each side the corresponding trunk cord has become resolved into its petal and stamen components. On the three other radii the stamen bundles, after having become detached, have branched to provide the strands for a group of stamens, a group instead of a single member being formed on each petal radius. 7. Base of the gynoecium. The sterile carpels no longer extend to the central tissue and each loculus, therefore, is now one chamber. In the centre, on the alternate (petal) radii, the placental strands in line with the persistent septa formed by the fertile carpels. All from transverse sections. Those in series magnified equally, except 4, which is less highly magnified than 3.

The outer sterile members form septa which, though at first complete, cease almost immediately to extend to the centre, and are gradually withdrawn completely into the ovary wall. The fertile carpels form the persistent complete septa on the alternate radii. An examination of the vascular system shows that below the ovary one set of trunk cords issues on each set of radii. The earliest to arise furnish the sepal midribs and the bundles for the antesepalous stamens; those arising later on the alternate radii provide sepal commissural marginals, petal midribs, and antepetalous stamen bundles. The fact that in *indica* the androecium complement on the petal radii consists, not of a single stamen, but of a group, does not affect the disposition of the carpel

whorls, for on neither set of radii do the strands for the stamen complement arise independently from the central cylinder. The groups are supplied in precisely the same way as the single members on the alternate set of radii, viz. by a bundle detached from a trunk cord which has already left the central cylinder. That these bundles give rise on the one set of radii to a number of branches and on the other set of radii remain unbranched has not, therefore, any differential effect on the carpel ground-plan. Transverse sections of the flower base show the incomplete septa (sterile carpels) in line with the sepals and the persistent septa (fertile carpels) in line with the petals. Here the regular alternation of the issuing whorls of vascular bundles meets with no check, since only one cord turns out below the gynoeceum on each radius. There is, therefore, no 'blocking' effect, and the loculi naturally come into being on the sepal radii. The same relations are found in *L. floribunda*, the position of the loculi being incorrectly shown in Eichler's diagram (loc. cit. p. 474, fig. 197 B).

When *L. Flos-reginae* is examined microscopically, it becomes clear that neither Eichler's diagram (loc. cit. p. 475, fig. 199 B) nor Koehne's account (loc. cit. p. 11) give a true picture of the facts, for it is then seen that both stamen whorls are, in fact, present. But, whereas in *indica* and *floribunda* the antesepalous whorl consists of single members and the antepetalous whorl of bundles, here both whorls are composed of bundles which are in such close juxtaposition that they merge together. The vascular strands for the two whorls arise as in the two above-mentioned species, being carried out as components of the sepal and petal trunk cords, respectively. But while in *indica* and *floribunda* only a single unbranched strand is detached from the sepal cords, in *Flos-reginae* a number of strands arise from both the sepal and the petal cords, those arising from the petal cords being somewhat fewer and diverging more regularly to right and left of the mid-line. As a result, there appears to be a break in the staminal ring opposite each petal, the effect of which is to produce a delusive appearance that the androeceum is made up of only antesepalous groups. The outer carpels and the loculi, as described and as is to be expected, stand on the sepal radii. It is thus apparent that the ground-plan of *Flos-reginae* presents no difficulty, but follows the general rule and is in accord with the other species of the genus.

The above relations having been established for *Lagerstroemia* it remains to consider certain species of *Ammannia* which, like *Lagerstroemia*, have isomerous six-whorled flowers, but in which the loculi are undoubtedly antepetalous.

*Ammannia octandra* L. f. and *A. coccinea* Rottb. both have the formula  $K\ 4\ C\ 4\ A\ 4+4\ G\ 4+4$ . In these types the vascular scheme of the perianth and androeceum is similar to that in *Lagerstroemia*, but that for the gynoeceum originates in a different way. Immediately below the flower the vascular cylinder expands into a ring of eight bundles. Some elements from these bundles follow a centripetal course and after re-arrangement become organized

into the midrib bundles of the four sterile carpels on the radii of the petals, and into the corresponding bundles with their placental strands of the four fertile carpels which are antesepalous. The conditions determining the radial disposition of the carpels when the vascular development proceeds centripetally, as already noted, are less obvious than when the bundles for all whorls develop centrifugally. Possibly, when the process is centripetal fresh considerations must be taken into account. It may be, for example, that where, as here, the cross section is four-sided, the distance from the centre to the angles (petal radii) being greater than that from the centre to the flat sides (sepal radii), the outer carpels develop where there is most room, i.e. in line with the angles, and the loculi are consequently antepetalous.

Most species of *Ammannia*, however, unlike the two cited above, have only five-whorled flowers, the antepetalous stamens having disappeared. Now it is to be noted that the carpels and loculi are developed in the same positions in these species as in the isomerous six-whorled types. That is to say, the suppression of one of the whorls has not affected the position of the succeeding whorl. This, on the view here taken that the principle of alternation consists primarily in the alternation, not of members but of out-turning midrib-forming bundles, is to be expected. The suppression of petals or of antepetalous stamens, or even of both, will have no effect on the radial disposition of the carpels, when the vascular bundles of the suppressed whorls do not arise as independent bundles, but, as here, are conjoined with the commissural sepal marginals which in these reduced types are still developed.

#### MELASTOMATACEAE. (Fig. 5.)

In the Melastomataceae the loculi in  $K\ n\ C\ n\ A\ n+n\ G\ n+n$  types are almost without exception antesepalous\*. The flowers are in general perigynous, calyx, corolla, and androecium being united to form the flower tube, from which, in these types, the petals and stamens later become exserted at the mouth. Only a single set of trunk cords turns out from the central cylinder on each of the two sets of radii, the bundles for the antesepalous stamens and sterile carpels passing out conjoined with the sepal midrib bundles, and those for the antepetalous stamens being conjoined with the petal midrib bundles, hence the outer carpels and the loculi naturally arise on the radii of the sepals.

#### CARYOPHYLLACEAE.

Reference to this family has already been made above (pp. 295, 297). As, moreover, a detailed description of several isomerous six-whorled genera has been

\* I have been unable to obtain suitable material of *Rhexia*, which, with a formula of  $K\ 4\ C\ 4\ A\ 4+4\ G\ 4+4$ , is stated to have antepetalous loculi, but it may be presumed, if this statement is correct, that some modification of the vascular scheme will be found in this genus which accounts for this departure from the usual arrangement in this family.

given in an earlier account (12), p. 261, Diagrams A-D, and pp. 283-285, it will suffice here to re-state the general conclusion regarding the gynoeceum ground-plan, viz. that whenever antesealous loculi occur in such genera, as they do in the majority, certain structural features are present (e.g. gynophore and stipe), the effect of which is to tend to relieve congestion and thus permit alternation to continue throughout; but that where such features are absent a hitch occurs in alternation after the fourth whorl. As a result, the outer carpel (fifth) whorl develops on the petal radii and the loculi are antepetalous.

### STACHYURACEAE.

Here, again, as a full description has been given in an earlier account of the flower of *Stachyurus praecox* Sieb. & Zucc. (15), p. 633, and figs. 132-139, it is unnecessary to enter into detail. The bundles for all six whorls turn out independently as in the Caryophyllaceae. The stamens are borne on a lobed disk. As the antesealous lobes are longer than those on the petal radii the antesealous stamens are carried further out than the antepetalous whorl. This difference in disk development on the two sets of radii leading to diplostemony, together with the presence of a short ovary stipe provide the conditions which allow alternation to continue throughout and the appearance of the loculi on the radii of the sepals.

The examples cited in the preceding pages will suffice to indicate the condition in which antesealous loculi are to be found in five- and six-whorled hypogynous and perigynous isomerous types. The much larger class in which such types show antepetalous loculi and an obdiplostemonous androecium, include all or most of the genera in Geraniaceae, Oxalidaceae, Rutaceae, Zygophyllaceae, Crassulaceae, Ericaceae, Pirolaceae, and individual genera scattered in other families, e.g. *Francoa* (Saxifragaceae), *Aphanopetalum* (Cunoniaceae). I have already dealt fully elsewhere with the causes of this interrupted rhythm in five of the above-mentioned families (see (8), pp. 147-149, and (11), pp. 102, 103, 116, and fig. 19 (Geraniaceae); (8), p. 149, (10) and (11), p. 112, Diagrams 20 & 21 (Oxalidaceae); (15) (Rutaceae and Zygophyllaceae); (11), pp. 114, 115, and figs. 72-82 (Pirolaceae)), and shall therefore confine myself to illustrating the views here advanced from types belonging to three of the other families cited.

### CRASSULACEAE. (Figs. 1-4.)

*SEDUM* spp., *CRASSULA* spp. In these two genera we have another excellent example of the apparent anomaly that while some species may have two stamen whorls and others only one the loculi appear on the petal radii in both classes.

The gynoeceum in this family is apocarpous, though spuriously so, for the individual ovaries, unlike those of *Coriaria*, *Xanthorrhiza*, and *Cephalotus*,

prove not to be monocarpellary \*. In the monocarpellary ovary the vascular supply consists of a median (midrib) bundle arising on the corresponding radius, with or without lateral branches. Ovaries composed of  $\frac{1}{2}$  1  $\frac{1}{2}$  carpels receive in addition half the vascular supply of the neighbouring carpels lying on the alternate set of radii. An examination of the vascular ground-plan in the crassulaceous gynoecium makes it clear that two carpel whorls are present, and that each ovary is composed of one whole sterile carpel and half the fertile carpel on each side. Hence the flower in fully developed types comes into the six-whorled class. In the isomerous forms the loculi are invariably antepetalous and the two-whorled androecium is obdiplostemonous.

In a species of *Sedum* taken at random, viz. *S. altissimum* Poir., it was found that on the one set of radii the out-turning sepal midrib bundles are followed later by a set of trunk cords composed of two components, the antesepalous stamen bundle and the midrib bundle of a fertile carpel. This latter component bifurcates at the moment that it becomes detached, the two resulting strands turning at right angles to right and left respectively. This splitting in half is a necessary preliminary to the halving of the fertile carpels, which takes place by radial splitting from without inwards and leads to the condition of spurious apocarpy characteristic of the family. Similar spurious apocarpy is to be seen in some Ranunculaceae (e.g. *Paeonia*, *Helleborus*, *Eranthis*) and in many Rutaceae (see (15)), but in the latter family the splitting is often only partial. On the alternate set of radii only a single set of bundles turns outwards. These bundles are trunk cords made up of four components, viz. the sepal commissural marginals, petal midrib and antepetalous stamen bundles, and the midrib bundle of a sterile carpel. Here we have the clue to the position of the stamens and loculi. The carpel midrib bundles on the petal radii are carried out in the first strands to leave the central cylinder on these radii; those for the carpels on the sepal radii form part of the second whorl of strands, hence the outer whorl of carpels and the loculi develop on the petal radii. Obdiplostemony naturally results, being further facilitated by the fact that the antepetalous stamen bundles are also carried out with the petal midrib bundles, whereas the antesepalous stamen bundles turn out independently of, and later than, the sepal midrib bundles. Furthermore, it follows that with such a vascular scheme the suppression of one component of the antepetalous trunk cords and of the member which it serves will not affect the radial position of later whorls. This is shown in the genus *Crassula*, and in the section *Procrassula* of the genus *Sedum*, in which, though the antepetalous stamens are lacking, the sterile carpels and the loculi remain antepetalous.

\* At the outset of the present series of investigations of the gynoecium, before I had extended my observations on apocarpous types beyond some of the genuinely apocarpous (monocarpellary) forms in the Ranunculaceae I instanced the Crassulaceae, following the traditional view, as also coming into this category. Later, however, I pointed out that a final statement as to the true nature of the Crassulaceous gynoecium must await a more detailed examination of the vascular scheme (see (8), p. 126, and (9) p. 623).

## ERICACEAE.

Almost all the types included in Ericaceae belong to the six-whorled isomerous category, and these invariably have antepetalous loculi and are obdiplostemonous. With few exceptions, the bundles for the members of all whorls turn out independently. The conditions are thus precisely those which are envisaged as leading to a condition of block and which, in all cases so far observed where other counterbalancing features do not nullify the natural result, lead to antepetalous loculi: and when the two carpel whorls differ in radial diameter to obdiplostemony.

The genus *Rhododendron* is exceptional in that the antepetalous stamen bundles do not arise independently but are carried out conjoined with the petal midrib bundles. Some species develop the full six whorls, but in others the antepetalous stamen whorl is suppressed (e.g. *R. indicum* Sweet. Again, we see the same apparent anomaly as has been described above in the genus *Sedum*. For in *Rhododendron*, as in *Sedum*, the loculi are antepetalous both in the five-whorled and the six-whorled species. Here, as in Crassulaceae, this apparent anomaly ceases to be such when viewed in the light of the vascular ground-plan.

## SAXIFRAGACEAE.

The Saxifragaceae, unlike the Crassulaceae, includes only a small number of six-whorled types which are isomerous throughout. Among such is the genus *Francoa*, which we may take as illustrative of this class. The vascular scheme here is in essentials similar to that of *Sedum*, with the difference that the *Francoa* flower is usually tetramerous. The bundles for the anteseptalous stamens turn out independently. On the petal radii the sepal commissural marginals, petal midrib, antepetalous stamen bundle, and sterile carpel midrib are all organised from the same cord. Hence, as in *Sedum*, the loculi are antepetalous and the flower obdiplostemonous.

## MONOCOTYLEDONS. (Figs. 8-15.)

In six-whorled isomerous Monocotyledons the arrangement of the vascular elements immediately below, and at, the flower base varies considerably, notwithstanding that the floral formula may be the same in all. In many types the summit of the flower stalk shows six bundles regularly arranged, one bundle lying on each of the six construction radii. In the simplest case, as e.g. in *Mayaca*, these six bundles become organised without any further process of rearrangement into the midrib bundles of the members successively formed on each of these radii. In other types, e.g. *Zebrina pendula* Schnizl., *Tradescantia virginica* L., *Commelina coelestis* Willd., an irregular rearrangement of the vascular elements presenting no definite pattern precedes the organisation of the midrib bundles for the outer whorls. In yet other types, e.g. *Melanthium*, a central group of vascular elements not obviously organised

into separate bundles is present in addition to an outer regular ring of six bundles. Of these differences we need not, however, take further account except in so far as they appear to be connected with the manner of origin of the midrib bundles for superposed whorls, i.e. whether these bundles arise independently or as components of trunk cords.

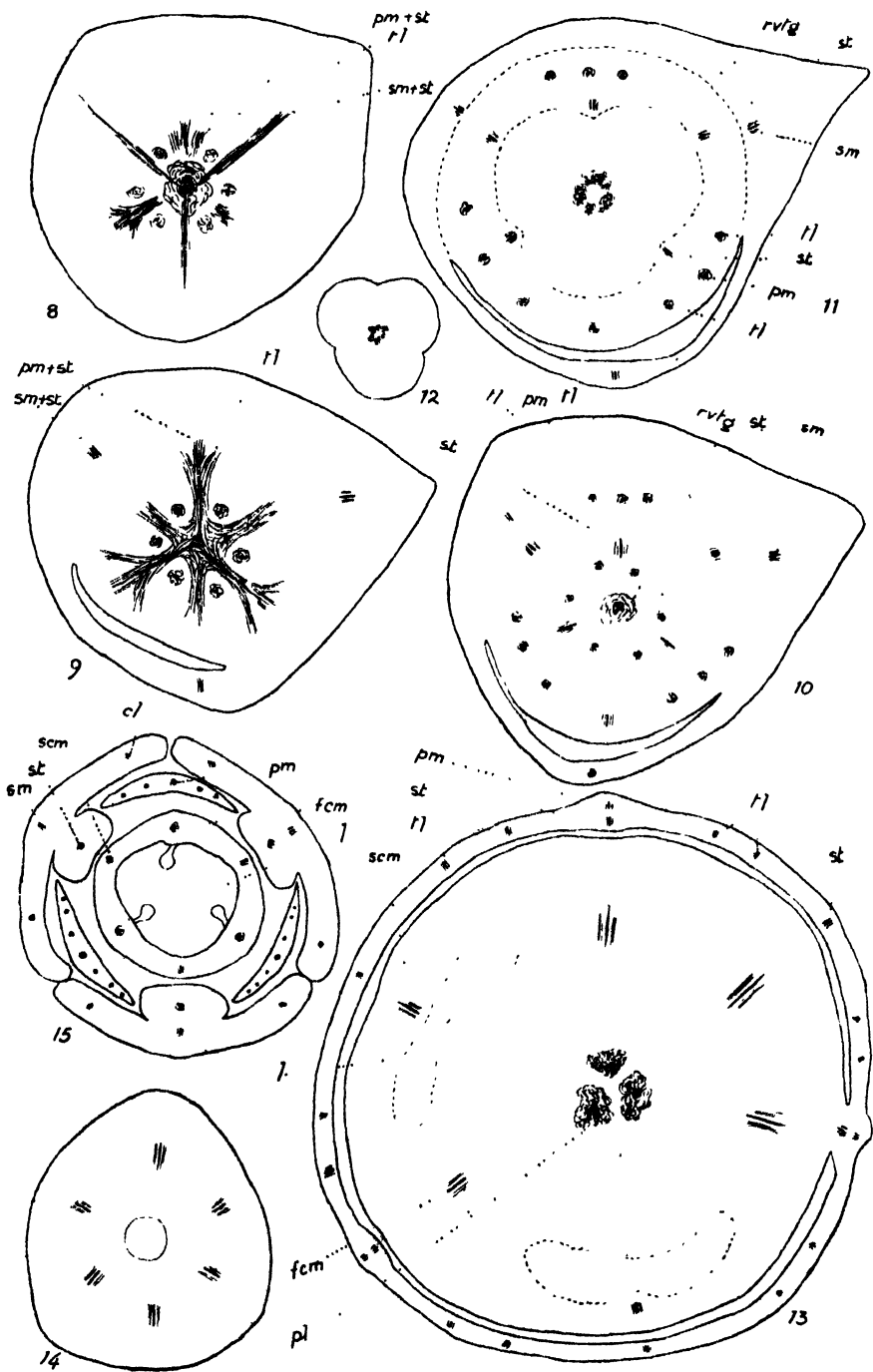
### LILIACEAE, COMMELINACEAE, FLAGELLARIACEAE.

(Figs. 8-12.)

*HYACINTHUS ORIENTALIS* L., *NARTHECIUM OSSIFRAGUM* Huds., *MUSCARI COMOSUM* Mill., *APHYLLANTHES MONSPELIENSIS* L. P 3+3 A 3+3 G 3+3. The antesepalous stamen bundles pass out conjoined with the sepal midrib bundles, and the antepetalous stamen bundles are similarly carried out conjoined with the petal midrib bundles. Here the conditions which have been envisaged as setting up a state of 'block' and causing a hitch in the regular alternation of the whorls after the fourth whorl are not present, hence the outer carpel bundles turn out in regular alternation on the radii of the sepals and the loculi are antesepalous. This is probably the most frequently occurring type of vascular scheme among six-whorled isomerous Monocotyledons.

*MELANTHIUM VIRGINICUM* L. P 3+3 A 3+3 G 3+3. As noted above, the flower stalk shows a peripheral ring of six bundles and a central group of vascular elements. The three bundles on the one set of radii, after turning outwards, give rise by simple disjunction to the sepal midrib, antesepalous stamen, and outer carpel midrib bundles. Those on the other set of radii, after turning outwards, similarly dissociate into the sepal commissural marginals, petal midrib and antepetalous stamen bundle, while the group of central elements becomes organised into the fertile strands of the three inner carpels. Here, again, where only a single trunk cord turns outwards on each radius to supply the perianth and androecium, it is natural that radial extension of the gynoecium should take place first on the sepal radii, and that if the outer carpel midribs are carried out as components of one set of the perianth-stamen trunk cords, these cords should be those on the sepal radii and thus that the loculi should be antesepalous.

*ZEBRINA PENDULA* Schnizl. K 3 C 3 A 3+3 G 3+3. From three of the six bundles present at the top of the flower stalk, after a process of reorganisation, a sepal midrib bundle and an antesepalous stamen bundle are successively initiated and turn outwards. In a similar manner the petal midribs and antepetalous stamen bundles are derived from the three bundles on the alternate radii. Both whorls of stamens are exerted from the perianth tube which becomes disjoined from the gynoeceial tissue below the level at which the outer carpel midrib bundles turn outwards prior to the appearance of the loculi. This early separation of the gynoeceial from the surrounding tissue has the same effect as a very short stipe. It prevents congestion and allows continued alternation of the whorls and the consequent formation of the loculi on the radii of the sepals.





## EXPLANATION OF FIGS. 8-15.

- 8-12. *Commelinaceae*. *Zebrina pendula* Schnizl. 8. Flower base after the sepal midrib bundles have turned outwards; those for the petals, which branch at once, are in process of turning outwards. 9. The same at the level at which the calyx is becoming exerted. Near the periphery the sepal midrib bundles. Nearer the centre on the same radii the antesepalous stamen bundles; on the alternate radii the branched midribs of the petals. Alternating with these six bundles the residual strands which, after reorganisation, give rise to the carpel bundles. 10. The same after the antepetalous stamen bundles have turned outwards. 11. The same at the level at which the gynoecium has become delimited, but is not yet disjoined from the corolla-stamen tube. In the centre the residual vascular elements not yet organised into the carpel bundles. 12. Base of the free gynoecium. The sterile carpel midribs are in process of being delimited, but have not yet turned outwards and the loculi have not yet made their appearance. 13. *Rapateaceae*. *Rapatea paludosa* Aubl. The flower after exertion of the calyx and just before complete disjunction of the gynoecium from the corolla-stamen tube showing the antesepalous position of the sterile carpels and the loculi which are becoming defined. 14, 15. *Mayacaceae*. *Myaca* sp. 14. Flower base showing the simplest type of vascular scheme in the isomerous Monocotyledon with one vascular cord on each of the six construction radii. In the centre the cavity which becomes the loculus. 15. The flower after calyx, corolla, and gynoecium have become disjoined. The vascular cords on the one set of radii have been resolved into sepal midrib, antesepalous stamen bundle and sterile carpel midrib, those on the alternate radii, similarly, into sepal commissural marginals, petal midrib and fertile carpel bundle. All from transverse sections. Those in series equally magnified, except 12, which is less highly magnified than the preceding figures.

*TRADESCANTIA VIRGINICA* L., *COMMELINA COELESTIS* Willd., *FLAGELLARIA INDICA* L. K 3 C 3 (or P 3+3) A 3+3 G 3+3. In these types the antesepalous position of the outer carpels and loculi is the outcome, not of the exceptionally early separation of the tissues of the outer and inner whorls as in *Zebrina*, but of the 'condensed' vascular scheme, for in all three types the stamen bundles are initiated from the same original strand as the midrib bundle of the perianth member on the corresponding radius.

*TOFIELDIA PALUSTRIS*. P 3+3 A 3+3 G 3+0. Here antesepalous loculi and a diplostemonous androecium are to be expected, apart from considerations of vascular anatomy, since only five whorls are present, one carpel whorl alone being developed. But the vascular scheme would also independently ensure this result, for sepal midrib, antesepalous stamen bundle, and carpel midrib bundle with its placental strand are all organised from one cord, while petal midrib and antepetalous stamen bundle are similarly derived on the alternate radii from a single cord.

## RAPATACEAE. (Fig. 13.)

*RAPATEA PALUDOSA* Aubl. K 3 C 3 A 3+3 G 3+3. As noted above (p. 297), Seubert's floral diagram of *Rapatea paludosa*, which appears in the 'Flora Brasiliensis' (16) and has been reproduced in later botanical works,

is incorrect in representing the loculi as antepetalous. Were this the true relation it would constitute the solitary example, so far as I am aware, of this arrangement among hypogynous Monocotyledons with a six-whorled flower. But material which I have examined shows unmistakable antesepalous loculi as was to be expected. Owing to the fact that the flower is ensheathed by numerous bracts the vascular arrangement at the summit of the flower stalk is much more complex than that found in any of the preceding types. It is possible, however, to determine that petal midrib, antepetalous stamen, and fertile carpel midrib are organised from a single cord on the one set of radii, though the last-named component soon comes to an end. The numerous strands entering the sepals are difficult to trace, but they appear to be derived from the same cords on the alternate radii as the antesepalous stamen bundles and sterile carpel midribs.

#### MYACACEAE. (Figs. 14, 15.)

MYACA sp. K 3 C 3 A 3+0 G 3+3. *Myaca*, like *Tofieldia* (see above, p. 311), has a five-whorled flower, but here it is the antepetalous stamen and not a carpel whorl which is lacking. This genus also differs from the preceding types in that the gynoeceum is unilocular with (so-called) parietal placentation. The vascular scheme of the flower reaches the limit in simplicity. A ring of six vascular cords regularly arranged is found at the summit of the flower stalk. The three cords on the one set of radii become dissociated into the sepal midrib, antesepalous stamen, and sterile carpel midrib bundles; those on the alternate radii similarly break up into the petal midrib and fertile carpel bundles. Since the bundles for all the members on any one radius are fused at their origin into a single cord it is obvious that the suppression of an earlier whorl will not affect the radial disposition of later ones. In transverse section the appearance at every level is diagrammatic in its perfect regularity.

From the various illustrative cases cited above it will be evident that the conditions which are visualised as bringing about antepetalous loculi and an obdiplostemonous androeceum in most hypogynous isomeric six-whorled Dicotyledons are absent in the Monocotyledon, where vascular fusions superposed upon the basal rhythm of vascular development on alternate sets of radii obviate the hitch in alternation which occurs in so many Dicotyledons of this class.

In all the types so far considered the curtailment of 'ground' space, resulting from the shortening of the floral axis, has been met either by a halt in the regular rhythm leading to superposition of two successive whorls or more frequently by economising time (vertical space) by means of the 'trunk cord' method of vascular development. We may conclude this account by comparing with these types a representative of that infinitely larger class, where adjustment has been achieved by reducing the number of floral members in the inner whorls,

## HYPERICACEAE. (Figs. 16-33.)

A more instructive example of this relation between reduction in the floral formula and restricted 'ground' space can scarcely be instanced than that of *Hypericum* where stages in the process of reduction can be traced in individual species. Within this genus are to be found the completely isomerous pentamerous form and grades of reduction viewed hitherto as conforming to the following formulae :—

$$(1) K 5 C 5 A 0+5^* G 5+5^*,$$

$$(2) K 5 C 5 A 0+5^* G 3+3,$$

$$(3) K 5 C 5 A 0+3^* G 5+5,$$

$$(4) K 5 C 5 A 0+3^* G 3+3.$$

Of these four classes (2) includes only a few species and (3), so far as I am aware, but one, of which I have been unable to obtain suitable material for investigation. The remaining species, about two hundred, fall into classes (1) and (4). A microscopic examination of representatives of these two latter classes enables us to understand why the above reductions have occurred in the androecium and gynoecium and to follow the precise manner in which they have been brought about.

*H. Hookerianum* Wight & Arn. may be taken in illustration of the isomerous pentamerous class. Transverse sections show that five vascular bundles leave the central cylinder at the flower base. These provide the five sepal midribs, which shortly develop a true branch system. The whole of the residual vascular tissue consists of five stout cords, horseshoe-shaped in cross section, on the alternate set of radii. From the mid-point of the convex arc of each of these residual cords a strand turns outward, which at once bifurcates, giving rise to a commissural marginal for the sepals on either side. These strands are immediately followed by the petal midrib bundles, which issue from the same primary cords without further reorganisation, being formed from the elements bordering the gap left by the preceding outgoing strand supplying the sepal commissural marginals.

After the emergence of the petal bundles another strand turns out from the same primary cords, again without any intervening reorganisation, and again from the elements bordering the gap left by both of the preceding outgoing strands. Each of these new strands branches copiously, the resulting group of branches supplying a corresponding number of stamens. Hence the five stamen groups, contrary to the usual arrangement of alternating whorls, stand in line with the petals. No strands for the androecium turn outwards on the alternate (sepal) radii, nor are any antesepalous stamens present. From the remaining elements forming part of each of the original primary antepetalous cords lateral strands develop which, running horizontally right and left, extend until they come into contact forming a new continuous ring

\* In these formulae  $\times$  is to be understood to stand for any number greater than one.



## EXPLANATION OF FIGS. 16-26.

**Hypericaceae.** 16-18. *Hypericum Hookerianum* Wight & Arn. 16. Flower base. At the periphery the ring of calyx bundles comprising the midrib bundles with true laterals and on the alternate radii the commissural laterals. Nearer the centre the five residual cords from which the bundles for the succeeding whorls are organised. 17. The same showing the sepals in process of exsertion. Within the calyx ring in the left half the bundle systems of three petals; those for the two in the right half not yet fully organised. 18. The same after exsertion of the calyx, and three of the five petals. On the left two of the five groups of staminal filaments (the bundle in each filament has been omitted); on the right the bundle systems for the other three groups. In the centre a residual vascular ring from which the five sterile carpel midribs, which branch at once, are turning outwards. 19. *H. lysimachioides* Wall. One of the central cords corresponding with those seen in 16, but more highly magnified, showing an early stage of delimitation into sepal commissural laterals, petal midrib, stamen bundle and the residual elements appropriated to the gynoecium. 20. *H. rhodopeum* Frivald. The same at a slightly later stage. 21-26. *H. Elodes* Huds. 21. Flower base. Towards the periphery in line with the angles the five sepal midrib bundles. Nearer the centre on the alternate set of radii the sepal commissural marginals and the petal midrib and stamen bundles in various stages of development from the original residual cords. Scattered irregularly between the stamen bundles the, as yet, unorganised strands destined for the gynoecium. 22. The same at the level at which the calyx ring is beginning to be exserted. Dissociation of the original cords on the petal radii is now complete. 23. The same at the level at which two of the petals and the intervening disk structure have begun to take shape. The staminal bundle in line with the petal on the left is isolated by the flanking gynoecium strands, but the two in line with the two upper petal bundles and the remaining two in line with the two lower petal bundles are not thus separated. 24. The same after exsertion of the petal seen in the mid-line below in 23. The approximation of the exsertion surfaces of this petal and of its neighbour on the right, and of the two superposed stamen bundles leaves no room for the development of a disk structure between them. 25. The same after exsertion of calyx and corolla. The same absence of an antesealous disk structure is noticeable between the exsertion surfaces of the two upper petals as is seen in 24 between the two lower petals, and is due to the same cause. The disposition of the xylem elements in the staminal bundles shows that the single stamen group supplied by the single bundle on the left will be composed of three members, the double groups above and below supplied by double bundles of four and five members, respectively. Towards the centre in line with the disk structures the three sterile carpel bundles are seen turning outwards; those for the fertile carpels are not yet organised. 26. The three stamen groups from another flower immediately after exsertion. A, a single group of three stamens, B and C, double groups, each of four stamens. All from transverse sections taken, when in series, from below upwards. All those from one species magnified equally.

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of five arcs centred on the sepal radii. After this reconstruction process a bundle turns outwards from the centre of each arc and becomes the midrib bundle of a sterile carpel, hence sterile carpels and loculi are antesealous. The elements of the recently formed ring which still remain become consolidated on the alternate (petal) radii, and are organised into the fertile carpel bundles.

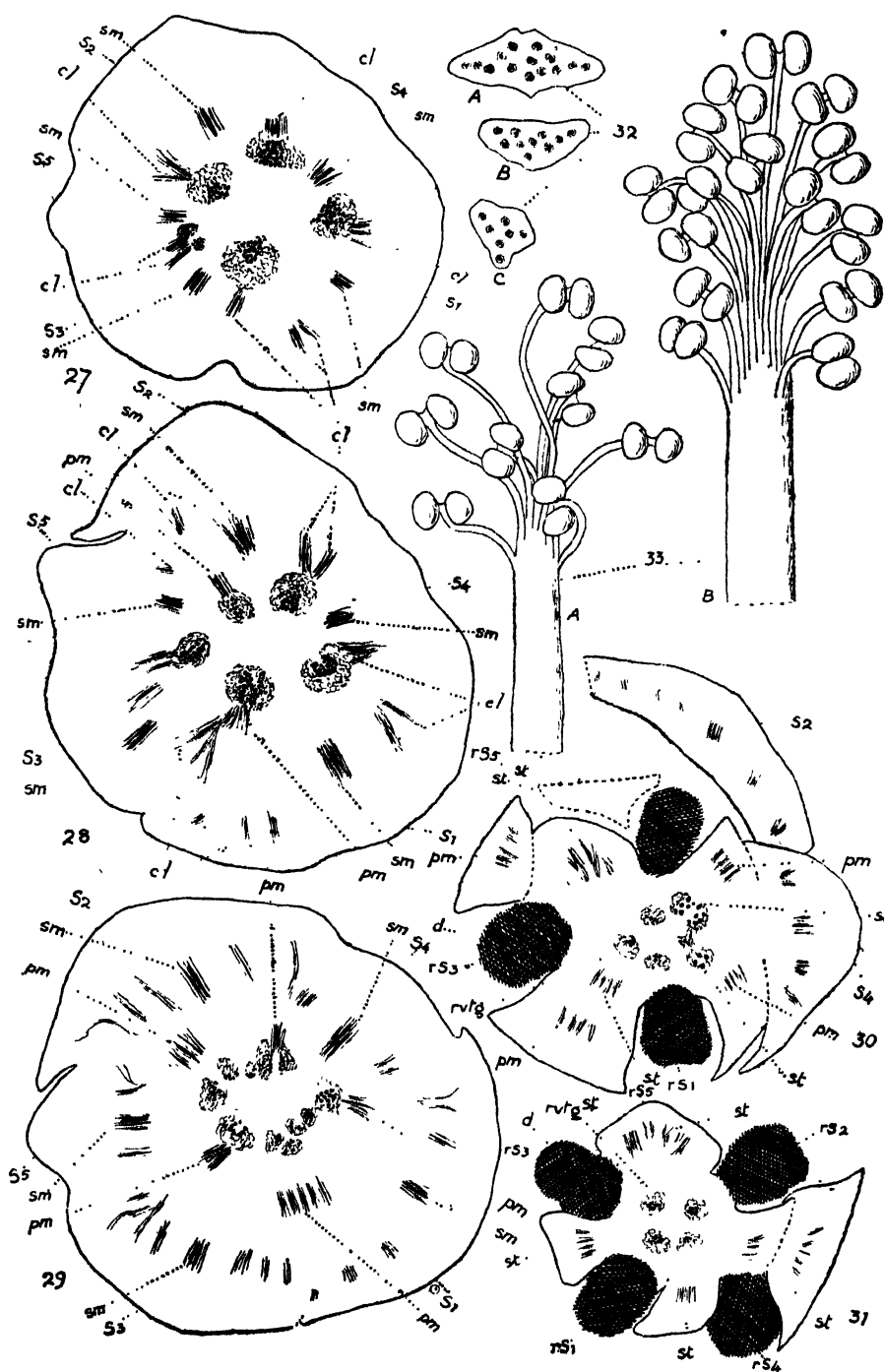


Here we have a type, isomerous throughout, in which there is a hitch in alternation between the second and third whorls. The reason for the superposition of these two whorls is clear. Sepal commissural marginals, petal midribs, and stamen bundles all originate from the same vascular unit, and although they turn out in succession there is no reorganisation between whorls. This unit, the central arc of the original horseshoe-shaped cord, is delimited as a whole from the residual elements, which will be reorganised to provide the midrib bundles for the succeeding (=carpel) whorls. Hence, from the aspect of the principle underlying alternation, petals and stamens together will behave as a single whorl and will be superposed.

Examples of class (4) which were examined included *H. Elodes* Huds., *H. aegypticum* L., *H. Coris* Beib., *H. humifusum* L., *H. reflexum* L., and *H. orientale* L. From the accompanying Table it will be seen that the relations here described hold good whether the stamens in the groups be many or few.

The manner of origin of the bundles for calyx, corolla, and stamens is the same as in the isomerous pentamerous forms. Here, however, the ground space is so restricted that, after the emergence of the sepal and petal bundles, some of the separate residual groups of elements from which the stamen bundles originate shortly come into contact. Typically, only one of these five group continues as a separate and distinct unit, the other four groups becoming consolidated in pairs into two larger groups. Consequently, only three groups of stamens are produced, the number of individual stamens in the two larger groups, though more than that in the single group, is usually less than twice as many.

Exceptional flowers now and again occur in which the androecium and gynoecium whorls are tetramerous ( $A\ 0+4^x\ G\ 4+4$ ). In these flowers three of the separate groups of vascular elements from which the stamen strands originate remain distinct, the other two alone becoming continuous to form one single large group. Now it is obvious that as the sepals arise successively, with a divergence of  $2/5$ , the available 'ground' space will decrease with the development of each successive member, and that the congestion or crowding will be most marked in the region of the two last sepals (4 and 5) and will be greater in the neighbourhood of sepal 5 than of sepal 4. It was found that in the exceptional flowers, in which only one pair of the groups of vascular elements giving rise to the main stamen strands become fused into a single group, this pair is always made up of the two groups situated, respectively, on each side of sepal 5. And that when two pairs of these groups of elements become single large groups, as in the type form, the two groups of elements making the second pair are those situated, respectively, on either side of sepal 4. Furthermore, the number of stamens in the two double groups shows a similar relation to the area available, the double group in the sector of sepal 4 being generally more numerous than the double group in the sector of sepal 5, as will be seen from the counts listed opposite.





## EXPLANATION OF FIGS. 27-33.

*Hypericaceae* (continued). *Hypericum aegypticum* L. 27-31. From an exceptional flower having a normal pentamerous perianth, but a tetramerous androecium and gynoecium. 27. Flower base. On the one set of radii the five sepal midrib bundles, on the alternate radii the five residual cords from which the sepal commissural laterals have already been organised and have turned outwards. 28. The same at the level at which the petal midrib bundles are becoming organised from the original residual cords and are turning outwards. 29. The same after all the petal bundles are completely organised, some having given rise to branch systems. 30. The flower after three of the sepals (not shown) and one of the petals (shown in position) have been exerted. The exertion surfaces of the two petals above on the left and the bundles for the two stamens lying on these radii are situated so near together that no disk structure develops on the intervening radius. The bundles for the two stamens on the right are not yet completely detached from the adjacent residual strand appropriated to the gynoecium. 31. The same after exertion of both perianth whorls with the exception of one petal. The bundles for all five stamens have now turned out to the periphery. In the centre the residual vascular strands for the gynoecium not yet organised into the carpel bundles. 32. The three stamen groups at the exertion level, from another flower. A and B, double groups of 14 and 10 stamens, respectively. C, a single group of 7 stamens. 33. Two staminal groups from a third flower. A single group of 9 stamens. B one of the two double groups with 15 stamens. All from transverse sections except 33. When in series taken from below upwards and magnified equally.

A more striking illustration of the direct relation between reduction in number and restriction of space could hardly be forthcoming.

It follows from the above facts that the usual floral formula for the three-bundled androecium of these species does not express the real position, since it implies that two bundles of stamens have disappeared, whereas, in fact, they are present but are fused with their neighbours. This relation would be made apparent by substituting the formula  $A 0+5 (1^x+2^y+2^z)$  for  $A 0+3^x$ .

Another effect of the restricted ground space is the non-development of the disk structure in line with sepal 5, and also, as a rule, of the one in line with sepal 4. It has been questioned whether these structures may not represent staminodes. But it must be emphasised that they have the usual form of disk (axial) outgrowths, that they are non-vascular, and that did they, in fact, represent an antesealous stamen whorl, we should expect the outer carpels (and loculi) to stand in line with the surviving stamen groups, seeing that these groups and the petals together behave in the scheme of alternation as a single whorl, but they are, in fact, situated on the other set of radii.

The reduction in the number of disc structures from 5 to 3, and a like reduction in the androecium ground-plan from 5 single units to 1 single and 2 double units, sets up a trimerous scheme which is continued in the succeeding carpel whorls ( $G 3+3$ ). In the exceptional flowers with four antesealous disc structures and four alternating groups of stamens\*, the gynoecium has a

\* Such flowers are of very common occurrence in *H. aegypticum*.

corresponding construction ( $G 4+4$ ). In such flowers the numbers of stamens in three of the groups differ but little from one another, but in the remaining group, which is a double group, the number is considerably larger.

We have then in *Hypericum* not only another excellent illustration of the value of the vascular ground-plan in elucidating the floral ground-plan, but further proof that the rhythm of alternation is based on a rhythmic alternation of whorls of organised and delimited *vascular units* and that whether such alternation is accompanied by alternation of the whorls of *members* depends upon the developmental potentiality of these strands: whether in constitution they are simple bundles and serve a single whorl, or are trunk cords which are later resolved into their components which become the midribs of different whorls. In the latter case superposition of the corresponding members will occur, notwithstanding that they belong to successive whorls.

#### SUMMARY AND CONCLUSIONS.

1. The generally accepted view that the successive whorls of members in isomerous cyclic flowers normally alternate throughout is true only up to a point.

2. It therefore becomes unnecessary to assume, where there is no evidence to support such an assumption, that the superposition of two successive whorls must be due to the suppression of an intermediate whorl.

3. The fundamental rhythm of the cyclic flower is that of the alternation of the whorls of vascular strands which are organised and delimited from the elements of the central cylinder and which become, or furnish, the midrib bundles of the floral members.

4. When the strands which become the midrib bundles of the members of successive whorls turn out from the central cylinder independently, then the whorls of members alternate throughout in flowers of less than six whorls.

5. When, in six-whorled flowers, the strands for all the whorls arise independently, a state of congestion appears always to be set up after the initiation of the fourth (second stamen) whorl, unless some special feature with a counter-acting effect is present. In consequence of this state of congestion, there is a check in the normal rhythm. When growth is resumed the impetus has apparently passed, owing to the inherent spiral rhythm, from the proper to the alternate set of radii, hence the fifth (outer carpel) whorl is superposed upon the fourth. After this check alternation again becomes practicable, the sixth (inner carpel) whorl alternating regularly with the fifth. The raising of the gynoeceum on a gynophore or stipe, or the early disjunction of the tissue of the outer whorls from that of the gynoeceum, prevents, it would seem, the occurrence of a state of congestion. Six-whorled types in which these features are present show alternation throughout.

6. Superposition of two successive whorls also occurs irrespective of the number of whorls present, and, even though the strands for the members of

the two superposed whorls turn out independently from the central cylinder, if they have originated from the same central cord and if the elements of the cord undergo no reorganisation between the emergence of the two strands.

7. Again, superposition of two successive whorls occurs if the strands for the members of the two whorls do not issue from the central cylinder separately but conjoined as one bundle which may then be looked upon as a compound bundle or trunk cord, possessing a twofold developmental potentiality. In these circumstances, as in those described in paragraph 6, the two whorls in question behave in the scheme of alternation as a single whorl.

8. The formation of the trunk cord affords a method alternative to that of reducing the number of members in a whorl by which cyclic forms have met the difficulty of restricted 'ground' space arising from the shortening of the floral axis. This alternative method, by which a saving is effected in vertical space, appears to be the one more commonly followed in Monocotyledons. In Dicotyledons a saving of space in the horizontal direction by reduction in the number of members in the innermost whorls, either alone or in conjunction with the trunk cord method, appears to be most usual.

9. The direct connection between lack of 'ground' space and reduction in the number of members in the whorls is particularly well seen in species of *Hypericum*, in which the stages in the process of reduction are easily followed. It is shown that in those species, which are regarded as having a trimerous androecium reduction from five bundles of stamens to three, is not due to suppression of two bundles but to the fusion of each of the two apparently missing bundles with a neighbouring bundle. These fusions occur where the crowding is greatest, viz. between the two bundles bordering sepal 5 and between the two bordering sepal 4. The effect of these fusions is that the pseudo-trimerous condition of the androecium is followed by a genuinely trimerous condition in the gynoecium.

10. A study of the vascular ground-plan is essential to a full understanding of the floral ground-plan. In particular, it affords an explanation of how it comes about that an intermediate whorl can be, and often is, suppressed without affecting the radial position of the succeeding whorl.

11. The conclusions summarised in the preceding paragraph are illustrated from types belonging to numerous families, including Coriariaceae, Ranunculaceae, Cephalotaceae, Elatinaceae, Lythraceae, Melastomataceae, Caryophyllaceae, Stachyuraceae, Crassulaceae, Ericaceae, Saxifragaceae, Liliaceae, Commelinaceae, Flagellariaceae, Rapateaceae, Myacaceae, and Hypericaceae. Incidentally it is shown that the current view of the floral ground-plan of *Lagerstroemia Flos-reginae* and *Rapatea paludosa* is incorrect in regard to the radial position of the loculi.

The accompanying figures were drawn by Miss D. F. M. Pertz, to whom I desire to express my very grateful thanks. I am also much indebted for material to the Director of the Cambridge Botanic Garden and to Dr. E. J. H. Corner, Mr. J. B. Stevenson, and Mr. E. M. Marsden-Jones.

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The structure of the ovary in the genus *Plantago* L.—I. The British species.

By RUBY E. DOWLING, M.Sc., F.L.S., Department of Botany, University College, London.

(With 3 Text-figures)

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IN the genus *Plantago* the ovary has been largely employed as a basis of classification. Barnéoud's (1) division of the genus into two sections, Polyspermae and Oligospermae, depended on the number of seeds in the pyxidium. Harms (7) questioned the practicability of this grouping, since the number of ovules reaching maturity is not constant in any one species. His classification in the main is that adopted by Decaisne (5), whose division of the genus into seventeen sections is based primarily on the habit of the plant, supplemented by the character of the ovary. Bentham and Hooker (3), while regarding the ovary as useful for classification of the genus, pointed out that it showed so much variation that it could not be utilised exclusively for this purpose: moreover, while recognising that the genus contains a number of natural species, they were of the opinion that these are so variable as to preclude the possibility of defining, with precision, either sections of the genus, or species.

A survey of the literature, however, reveals that there has been considerable diversity of opinion as to the structure of the ovary in the genus; and this is not to be attributed to the variation referred to above. Thus Lindley (10) writes: '[the] ovary [of the Plantaginaceae is] composed of a single carpel, sessile, without a disc, 2-, very seldom 4-celled, the cells caused by the angles of the placenta; . . . Capsule membranous dehiscent transversely with a loose placenta bearing the seeds on its surface'. Further, 'The ovary of *Plantago* does not present distinctly the appearance of a free central placenta. But, in reality the placenta is at first quite free, although eventually it is pressed close to the sides of the ovary, and thus divides the cavity into 2 or more cells. This is, however, only a temporary contact, for long before the seeds are ripe the placenta shrinks so much as to lose its adhesion with the sides of the ovary, and then it becomes truly free. In *Plantago arborescens* it is, when ripe continuous with the stigma, and the two become loose and may be removed together, leaving the sides of the ovary undisturbed'. This emphasis on the continuity of the placenta and stigma in the fruit of *P. arborescens* would suggest that Lindley regarded this condition as unusual in the genus. Bentham and Hooker (3) claimed that the ovary is bilocular or falsely 3-4 locular with

1- $\infty$  seeds in each loculus: the membranous capsule has two loculi or by abortion only one, while according to Harms (7) the ellipsoidal ovary is 2-(4)-celled with 1- $\infty$  seeds in each compartment. As far as the British species are concerned both Hooker (9) and Bentham and Hooker (4) state that the ovary is 2-4-celled, while Bentham and Hooker give the number of seeds as two or more. Further discrepancies come to light from a comparison of the specific descriptions of the British species (4, 9). These will be referred to later.

It has been shown elsewhere (6) that *P. Coronopus* L. has a bilocular ovary, which is apparently quadri-locular owing to the development of placental tissue between the seeds in each loculus: this placental tissue, however, is not fused with the ovary wall (cf. Bentham (2)). Further, it has been demonstrated that three seeds are produced in the anterior loculus, two below and one above, and that the upper and lower seeds are morphologically and biologically different, though both types are equally capable of reproducing the species. It has been noted that abortion of ovules is not frequent in this species: the majority of the capsules examined had five mature seeds, four below and one above. According to Hooker (9) this species has a 3-4-celled capsule with 3-4 seeds, while Bentham and Hooker (4) describe the ovary as 4-celled, each cell having a single ovule, although frequently only two mature seeds are found in the capsule. Thus the general consensus of opinion would appear to be that the ovary in this species is more than 2-celled. This condition, however, is due to the development of placental tissue between adjacent ovules in *each* loculus: this tissue reaches to the ovary wall, but does not fuse with it.

Longitudinal sections of the ovary show a similar development of placental tissue between the upper and lower seeds in the anterior loculus. While, however, the development of placental tissue between adjacent seeds accounts for the spuriously four-locular condition in *P. Coronopus*, the septum is in organic continuity with the ovary wall during the early stages of development: this is a true septum, dividing the ovary into posterior and anterior loculi. It is never unilocular with a central column of placental tissue, such as may be supposed to have occurred in an ovary of the type described by Lindley (10). Examination of longitudinal sections of the ovaries makes it clear that the placentation is axile, not free central, for the septum is joined to the ovary wall at the top as well as at the sides. Separation of the placental tissue from the ovary wall takes place at a comparatively early stage in the development of the capsule and when dehiscence occurs the lid comes away with the placental core inside it, separation of the tissue having taken place at the base of the capsule; the thin lateral walls are broken so that the four lower seeds are shed; the upper seed is held in the capsule lid until such time as the placental core comes away or, as is more usual, until both lid and placenta decay.

In *P. major* L. the ovary is also bilocular with an axile placenta, which remains joined to the ovary wall, at the top and bottom of the capsule, but

becomes free at the edges at a very early stage in development. The ovules completely cover the placenta except where this is joined to the capsule wall above and below: as the seeds enlarge they cover the ruptured edges of the placenta (fig. 2 D). In the placenta of the mature capsule there is a cleft which apparently develops as the fruit enlarges. There is no indication of a divided placenta in the young capsule of *P. major* such as is found in *P. maritima* (q.v.).

The number of seeds in each loculus is approximately equal and these seeds are arranged in general in two tiers one above the other (fig. 2 D) (c.f. Bentham (2)). The number of seeds produced in each capsule varies from as few as three to as many as twenty-eight. One thousand capsules were examined, and when the number of seeds was plotted against the number of capsules a bimodal curve for seed number was obtained with a mode at ten seeds per capsule, and a second mode at eighteen seeds per capsule (fig. 1 A). This bimodal curve for seed number suggests the possibility of the presence in this country of *P. major* var. *polysperma* Haass referred to by Hegi (8). In this variety the number of seeds in a capsule varies between sixteen and twenty.

This bimodal curve for variation in seed number may, however, possibly be accounted for by unconscious error of sampling. That the bimodal curve may not be a fair representation of a normal population is supported by the evidence afforded by the range of variation in seed numbers in the capsules of single inflorescences. An examination of fig. 1 B, in which this variation is plotted, will show that the mean values for the number of seeds per capsule in the different inflorescences form a continuous curve and do not fall into two groups, as might be expected if the bimodal curve for variation in seed number (fig. 1 A) were due to the presence of two strains of *P. major* in the sample. It is significant in this connection that in one inflorescence the range of the number of seeds per capsule was almost as great as that for the whole sample.

On the other hand, it may be urged that this bimodal curve does, in fact, indicate the presence of two strains of *P. major* in the material examined, and that these cannot be separated into two distinct groups on their seed number may be the consequence of hybridisation between the strains—a view supported by the wide range of variation in the number of seeds in a capsule exhibited by individual inflorescences.

Hegi (8) gives the seed number for *P. major* var. *polysperma* Haass as varying between sixteen and twenty, while the number of seeds in a capsule in the type-species varies between eight and sixteen. Thus, even if there were two strains present in the sample examined, the fact that the upper limit of seed number in the species corresponds with the lower limit of seed number in the variety may militate against a separation into two groups by means of seed number.

This remarkable and, at present, unexplained variation in seed number in *P. major* serves to emphasise the view that the ovary in the genus *Plantago* is of little value in defining either sections or species of the genus (c.f. (3)).

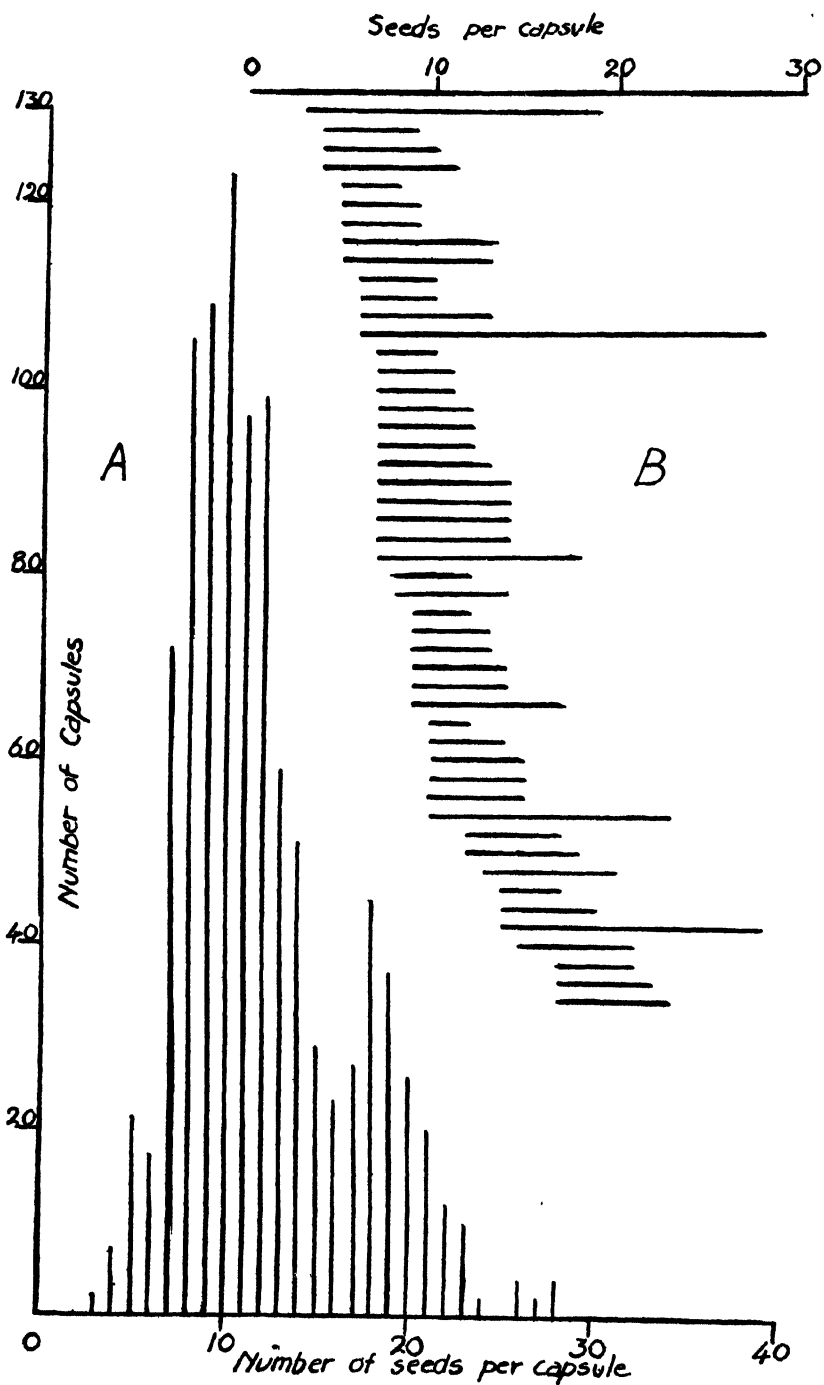


FIG. 1.—*Plantago major*. A. Variation in number of seeds per capsule in 1000 capsules. B. Range of variation in number of seeds per capsule in 49 inflorescences.



Hooker (9) states that *P. major* has a bilocular ovary with 8–16 seeds. It is thus interesting to note that of the 1000 capsules examined 30 per cent. showed a seed number outside the range given by this author. As might be expected in an ovary producing a large number of ovules abortion is frequent, as many as thirteen abortive ovules having been found in a single ovary. This abortion of ovules is not solely responsible for the low seed numbers in some capsules, because in those showing the lowest seed output there was no evidence of abortive ovules; in general, the tendency to abortion is more marked in those capsules with a high seed output. The description of *P. major* given by Bentham and Hooker (4) agrees in general with that of Hooker (9)—i.e. that the ovary is 2-celled with from 4–8 seeds in each cell.

Harms (7) places *P. major* in the section *Euplantago* Harms in which the capsule has from 6–18 small seeds with irregular edges: the inner side of the seeds is almost flattened. In this the description agrees with that given by Hooker (9), who also adds that the seeds are black and rough. In the material examined the seeds have a granular appearance, but can scarcely be said to have irregular edges (fig. 2 A) unless this be taken to mean that the seeds vary in shape. They do, however, show morphological polymorphism, which may be due to mutual pressure of the seeds in the capsule. While it is true to say that some of the seeds are flattened on the inner face, this is by no means always so, some of the seeds showing a marked median ridge on the inside and a convex face on the outside (fig. 2 A).

The placenta in *P. major* is in general fairly symmetrical in outline, having been attached to the capsule wall along the whole of its thin edge (fig. 2 C). Occasionally, however, placentae were found which resembled those of *P. Coronopus*, in which there was a depression in the thin edge of the placenta at the top of the capsule. An ovule was invariably attached to the placenta in this depression and recalls by its position the upper ovule in *P. Coronopus* (fig. 2 B) (c.f. (6) fig. 1 C).

In *P. major* the line of dehiscence is slightly below the mid-line between the top and bottom of the capsule (fig. 2 D), consequently, when the lid comes off, as it does without the placenta in this species (fig. 2 D), the upper layer of seeds will be shed immediately; the lower seeds will be held for a short time between the placenta and the ovary wall: in this way there may be a slight delay in the dispersal of the lower tier of seeds in *P. major*. The time which elapses between the shedding of the two layers of seeds may be so short as to be of no biological significance, but it suggests a tendency to delayed dispersal of some seeds, a tendency which finds further expression in *P. Coronopus* (Dowling (6)).

In *P. media* L. the ovary is bilocular (fig. 2 G, H), the axile placenta remaining attached to the top and bottom (fig. 2 J, K) of the capsule, although it becomes separated at the edges from the ovary wall at a very early stage in development. In general, there are three ovules in each loculus arranged in two series, which frequently overlap in such a way as to show all three ovules of a loculus

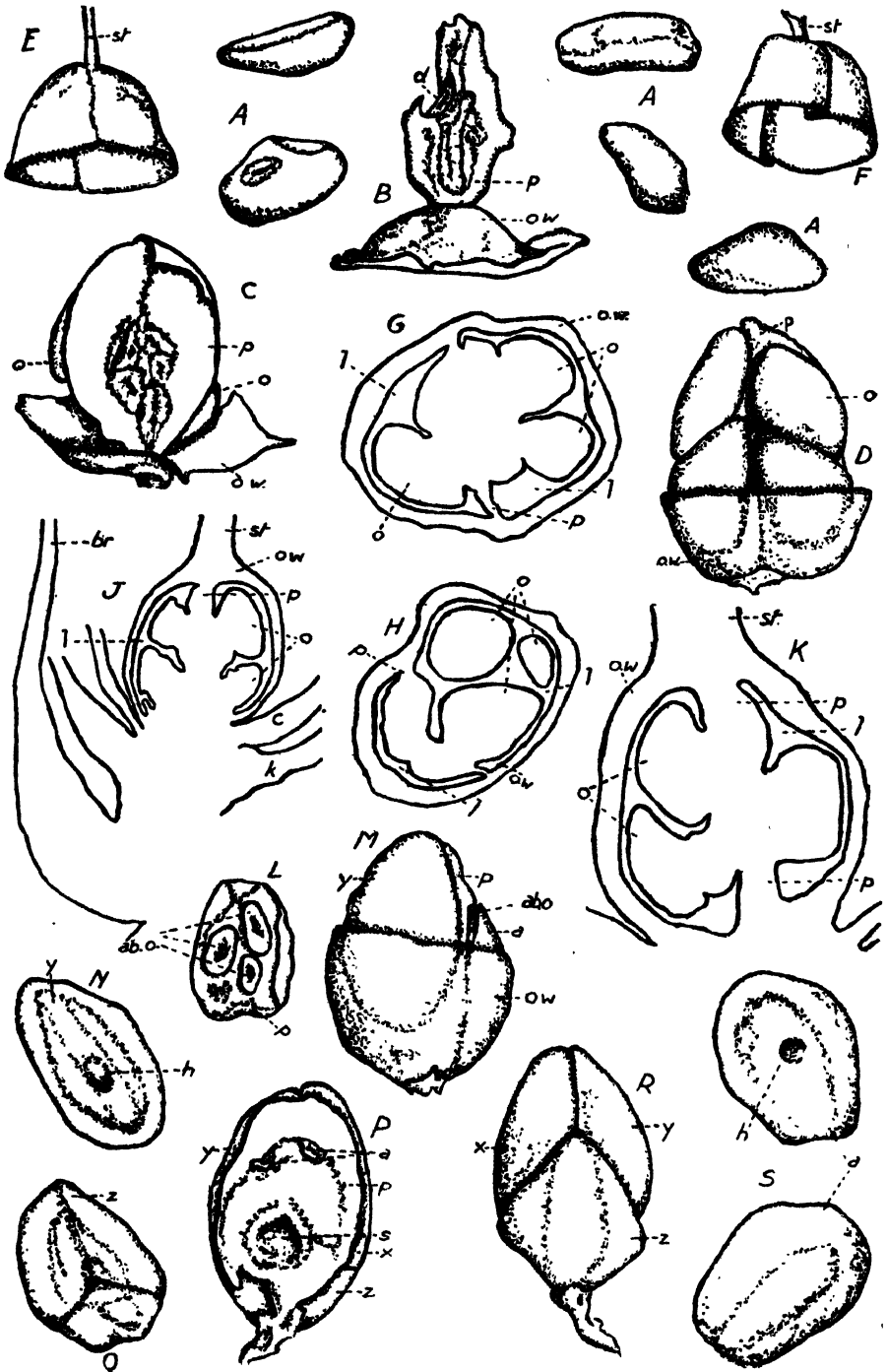


FIG. 2.

## EXPLANATION OF FIG. 2.

A-D. *Plantago major*. All  $\times 13$ .

- A. Immature seeds showing variation in shape.  
 B. Placenta with ovules removed showing depression (*d*) at top.  
 C. Placenta with ovules removed.  
 D. Capsule with lid removed showing ovules covering placenta.

E-S. *Plantago media*.

- E & F. Capsule lids showing various degrees of folding of wall.  $\times 13$ .  
 G & H. Transverse sections of ovaries,  $\times 25$ . G showing fertile ovules in both loculi.  
 H with fertile ovules in one loculus only.  
 J & K. Longitudinal sections of ovaries. J,  $\times 13$ ; K,  $\times 25$ .  
 L. Placenta to which are attached three abortive ovules which were present in one loculus of the ovary.  $\times 13$ .  
 M-S. Placenta and ovules from one capsule in which there were three fertile ovules in one loculus and one fertile ovule and two abortive ovules in the second loculus.  $\times 13$ .  
 M. Capsule with lid removed showing placenta and three ovules, two fertile (*a*, *y*) and one abortive.  
 N. Inner side of one of upper ovules (*y*) from loculus with three fertile ovules.  
 O. Inner side of lower ovule (*z*) from loculus with three fertile ovules.  
 P. Placenta showing scar of attachment of fertile ovule and the two abortive ovules.  
 Behind are three fertile ovules of the other loculus.  
 R. Three ovules from one loculus, attached to placenta.  
 S. Two views of fertile ovule from loculus with abortive ovules.

*a*, fertile ovule in loculus with two abortive ovules; *ab.o.*, abortive ovule; *br.*, bract; *c.*, corolla; *d.*, depression in top of placenta; *h.*, hilum; *k.*, calyx; *l.*, loculus; *o.*, ovule; *o.w.*, ovary wall; *p.*, placenta; *s.*, scar of attachment of ovule; *st.*, style; *x*, *y*, *z*, three ovules in one loculus.

in a median transverse section of the ovary. Two of the ovules in each loculus are usually found in the upper part of the capsule, the third is below and usually lies between the two upper ovules (fig. 2 R).

Very occasionally there are four ovules in a loculus, and under these circumstances there are two pairs of two ovules one above the other.

Three hundred and sixty capsules of *P. media* were examined and the seed numbers are given in Table I.

TABLE I.

	7 seeds.	6 seeds.	5 seeds.	4 seeds.	3 seeds.	2 seeds.	1 seed.	Total.
Unripe capsules ..	..	5	9	11	14	12	9	60
Mature capsules ..	1	8	21	59	68	90	53	300

Of the sixty unripe capsules examined thirty-seven showed six ovules, but in five capsules only, did all six ovules mature. Almost without exception some of the ovules in each capsule were abortive (fig. 2 L, P). The placental tissue in the mature capsules was very shrivelled and this rendered it difficult to ascertain with accuracy the number of abortive ovules, so that account was taken only of mature seeds. A few capsules produced fewer than six ovules ; thus in two capsules there were four and in two others five ovules.

Not infrequently all the ovules in one loculus were abortive (fig. 2 L), and this resulted in unequal enlargement of the two loculi comparable to the unequal development of the loculi in *P. lanceolata* (cf. p. 333), which results from the abortion of one of the ovules.

In addition to the complete suppression of all the ovules in one loculus one or two were abortive in the second loculus, giving the one-seeded condition found in sixty-two capsules. It was apparent that abortion occurred with equal frequency in upper and lower ovules.

The unequal enlargement of the seeds sometimes results in a folding of the wall of the capsule lid giving the appearance of ridges of tissue on the inside (fig. 2 E, F). These two folds simulate placental tissue, but are actually produced from the capsule wall, and their presence suggests that when the fertile seeds were enlarging the placenta was still attached to the wall of the ovary at the inner edges of the fold. The unequal pressure on the two sides of the placenta resulting from a difference in the rate of seed development in the two loculi would tend to push the placenta into the loculus in which seed development was proceeding more slowly. If the placenta be free at its edges this movement can take place without altering the shape of the capsule wall, but if the placenta be still attached to the fruit wall a folding, similar to that observed, might result.

If the folds observed in some of the capsule lids be due to this cause, then in *P. media* the bilocular condition of the ovary is at least occasionally retained beyond the earliest stages of ovary development.

A survey of the literature shows that there is more discrepancy in the descriptions of the ovary of *P. media* L. than in any other British species of the genus. Thus Decaisne (5) includes *P. media* in § *Lamprosantha*, in which the capsule is 4-seeded. Of *P. media* he says that the capsule is 4 or very rarely 6-8-seeded. Harms (7), following Decaisne, also includes *P. media* in the *Lamprosantha* section of the genus. No specific details are given for *P. media*, but the section is characterised by having a 4-seeded capsule in which the seeds are planoconvex.

Hooker (9) states that *P. media* has a 2-celled capsule which is 2-seeded, the seeds being flat in front.

In the key to the species of *Plantago* given by Bentham and Hooker (4) the capsule of *P. media* is stated to be 1-seeded, while the specific description reads : ' ovary with 2 seeds in each cell but they often do not all ripen and the capsule has then but 3 or 2 altogether '.

The seeds of the *P. media* examined vary to a certain extent in shape. Thus fig. 2 S shows the one lower seed produced in a loculus in which the two upper ovules were abortive (cf. fig. 2 M). The inner side of the seed is flat and the outer convex, thus agreeing with the description given by Harms (7) and Hooker (9). Fig. 2 N shows one of the upper seeds from the other loculus of the same capsule in which all three ovules were fertile: this seed also is plano-convex, although differing somewhat in shape from the seed from the other loculus. The lower seed in the loculus with three fertile seeds is shown in fig. 2 O. It is convex on its outer face (fig. 2 R, z), but shows three distinct ridges on the inner face corresponding with depressions on the placenta. In *P. media* therefore there is a marked tendency to morphological polymorphism of the seeds which may be the result only of mutual pressure of the seeds in the capsule. This polymorphism becomes more conspicuous as the seeds ripen.

In *P. maritima* L. the young ovary is bilocular, although the axile placenta becomes free at the edges during development. In the dissection of young ovaries of this species it was noticed that the placenta was divided into two parts at the top and was thus attached to the top of the capsule in two places (fig. 3 P, x, x). A placenta of this type is figured by Payer (11) for several species of *Plantago*, but I have noted it only in *P. maritima* (cf. *P. major* on p. 325).

Forty young capsules of *P. maritima* were dissected, and of these thirty-nine showed three ovules. Two of these ovules were side by side in one loculus, the other ovule was at the top of the capsule in the other loculus (fig. 3 T, U).

An arrangement of the ovules in the capsule similar to that described above has also been observed in nearly mature capsules. In some of these the two ovules, in one loculus, were well developed, while the upper ovule in the other loculus was abortive (fig. 3 M, N, P).

One hundred dry mature capsules were examined and of these ninety-six had only a single seed. Of the other four capsules each with two seeds, three had the lower seeds developed, both in the same loculus; in the fourth capsule the upper seed was developed and also one of the lower seeds, consequently in this capsule the two seeds were in different loculi. In these mature capsules the placental tissue had withered, so that it was not possible to identify abortive ovules with any certainty.

In one young capsule there were four ovules, one of these, in the loculus with the upper ovule, was abortive. This abortive ovule was below the fertile one in the same loculus and at the same level as those in the other loculus (fig. 3 R, S).

*P. maritima* is placed by Decaisne (5) in § Coronopus, in which section the capsule is sub 4-locular and 3-4-seeded. Harms (7) also includes *P. maritima* in the § Coronopus, in which the capsule is 2-4-seeded with fairly small planoconvex seeds. In the sub-section in which *P. maritima* is included the capsule is stated to be mostly 2-seeded.

Both Hooker (9) and Bentham and Hooker (4) state that the capsule is 2-celled

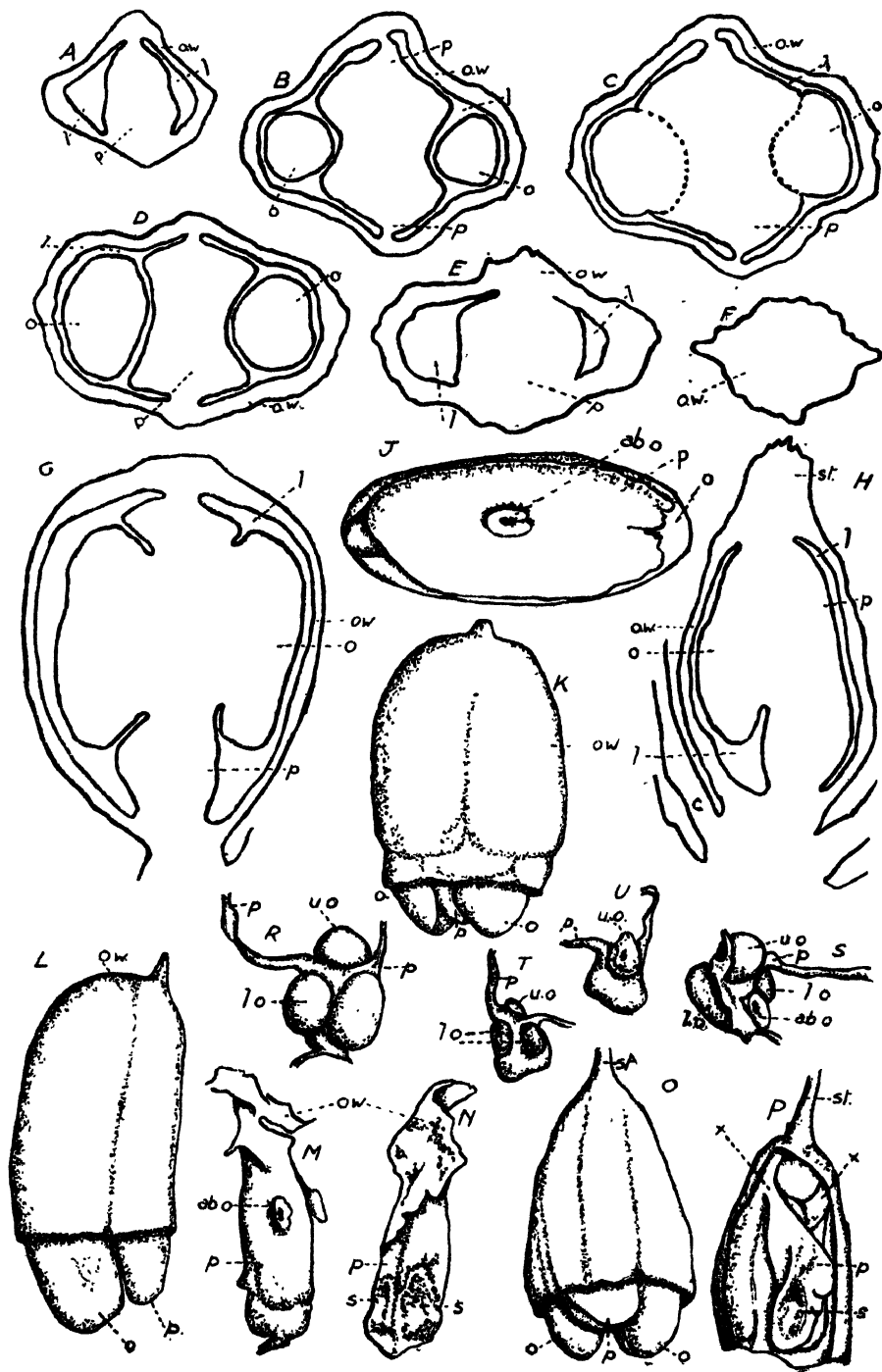


FIG. 3.

## EXPLANATION OF FIG. 3.

A-L. *Plantago lanceolata*.A-F. Series of selected transverse sections of an ovary from base to apex.  $\times 25$ .G & H. Longitudinal sections of ovaries showing axile placenta.  $\times 25$ .

G. Ovary with fertile ovule in each loculus.

H. Ovary with fertile ovule in one loculus—other loculus sterile.

J. Placenta removed from capsule showing fertile ovule (behind) and abortive ovule.  $\times 13$ .K. Capsule lid with placenta and fertile ovule in each loculus.  $\times 13$ .L. Lateral view of capsule lid with placenta and fertile ovule *in situ*.  $\times 13$ .M-U. *Plantago maritima*.M, N. Two views of placenta with part of ovary wall attached at top.  $\times 13$ .O. Capsule lid with placenta and two ovules *in situ*.  $\times 13$ .P. Capsule dissected to show placenta attached to top of ovary wall in two places (*x*, *x*).  $\times 13$ .R, S. Two views of placenta dissected from young capsule to show two lower fertile ovules in one loculus and upper fertile ovule in other loculus: abortive ovule also present in this loculus.  $\times 25$ .T, U. Two views of placenta dissected from young ovary showing upper fertile ovule in one loculus and lower fertile ovules in other.  $\times 13$ .*ab.o.*, abortive ovule; *c.*, corolla; *l.*, loculus; *l.o.*, lower ovule; *o.*, ovule; *o.w.*, ovary wall; *p.*, placenta; *s.*, scar of attachment of ovule; *st.*, style; *u.o.*, upper ovule.

and 2-seeded. I have not been able to confirm the arrangement of the ovules figured by Hegi (8), who shows transverse sections of a younger and older capsule in which there are two ovules in each loculus separated by placental tissue: one ovule in each loculus apparently develops to give the two-seeded condition, which is described as being typical of the species.

In *P. lanceolata* L. the ovary is bilocular (fig. 3 A-F) with an axile placenta which early becomes free from the capsule wall at the edges while remaining attached at both top and bottom (fig. 3 G, H). In each loculus there is a single ovule produced approximately in the middle of the flat face of the placenta (fig. 3 J). Sometimes both these ovules develop, but abortion of either the anterior or posterior ovule is frequent, giving an ovary which at maturity contains one fertile seed and one abortive ovule (fig. 3 H, J, L), cf. *P. media*, p. 330.

The ovule—or ovules, when both develop—increases in size and early extends beyond the edges of the placenta (fig. 3 J). When both ovules develop the placenta forms a comparatively thin plate of tissue between them (fig. 3 K), and separation of this placental tissue takes place at the base of the capsule before it does at the apex, so that the lid comes away from the lower part of the capsule with the placenta still attached. The seeds may fall out when the capsule lid becomes separated, or they may remain in it for a short time before being scattered.

When only one ovule matures the placenta occupies relatively more space in the capsule, and might easily be mistaken for an immature ovule in the unripe capsule (fig. 3 L). The abortive ovule is a small whitish structure with a dark centre on the flat face of the placenta between it and the ovary wall (fig. 3 J). Dehiscence of the capsule containing only one mature seed is similar to that of the capsule with two seeds.

Four hundred capsules were examined, and of these 44 per cent. showed two fertile seeds while 56 per cent. had only a single fertile seed. In one capsule there was a single fertile seed, but there was no evidence of a second ovule ever having been produced. The occasional complete suppression of one of the ovules in *Plantago* is significant in view of the single-seeded condition found in the fruits of the other genera of the family.

When both ovules develop, in general they do so simultaneously and equally, although occasionally unequal development of the two ovules was found; one sometimes being larger than the other and sometimes more mature, as evidenced by the change in colour of the testa.

There was a noticeable difference in the number of capsules showing abortion of one ovule in different parts of the inflorescence; the upper part in general showed a higher proportion of capsules with two seeds each (Table II). It is significant in this connection that *P. lanceolata*, in common with the other species of this genus, is very markedly protogynous, and it seems reasonable to assume that pollen might be more abundant when the stigmas of the upper flowers of an inflorescence were receptive than when those of the lower flowers were mature.

TABLE II.

Base of inflorescence.	Top of inflorescence.
37 per cent. capsules with 2 seeds.	52 per cent. capsules with 2 seeds.
63 per cent. capsules with 1 seed.	48 per cent. capsules with 1 seed.

In the literature there is agreement on the two-seeded capsule of *P. lanceolata*, but no mention is made of the frequent abortion of one of the ovules, which results in a one-seeded capsule.

A comparison of the British species of the genus *Plantago* would seem to indicate that they constitute a series showing increasing sterility in the ovary.

*P. major* has a bilocular ovary in which a considerable number of ovules are produced in each loculus. Abortion of some of these ovules does occur, but, even when allowance is made for this, the output of seed by each capsule is greater in *P. major* than in any other of the British species. In *P. major* there are regularly two tiers of ovules and seeds in the capsule.



*P. media* presents the next stage in the postulated reduction series. Here there is a bilocular ovary in which normally six ovules are produced—three in each loculus. These six ovules are in two rows one above the other, although in general there is only a single ovule in the lower layer. Sometimes all six of these ovules develop into mature seeds, but more frequently some smaller number matures. In this species both upper and lower ovules abort.

In *P. Coronopus* there is also a bilocular ovary and five ovules are regularly produced—two in the posterior loculus and three in the anterior loculus. Four of these ovules, i.e. the two in the posterior loculus and two in the anterior loculus, are similar in size and shape, and appear to represent the lower layer of ovules such as occurs in *P. major*. The fifth ovule in *P. Coronopus* is produced at the top of the capsule, and may reasonably be looked upon as representing the sole surviving member of the upper layer of ovules found in *P. major*. In *P. Coronopus* abortion is infrequent and does not involve the upper ovule.

In *P. maritima* there are usually only three ovules; two of these ovules are side by side in one loculus and are apparently lower ovules, the third ovule is in the other loculus and is nearer the top of the capsule—frequently only one seed matures. In one ovary examined there was a lower ovule in the second loculus which was abortive.

*P. lanceolata* apparently represents the culmination of the series. The ovary is bilocular, and in each loculus a single ovule is produced: there is no evidence to show whether these represent upper or lower ovules. In a certain proportion of the ovaries both these ovules develop: in more than half of those examined, however, one loculus of the fruit contained a fertile seed: in the other loculus the ovule was abortive. In one capsule the sterility of the ovary was carried a stage farther, for in this, although two loculi were formed, only one of them developed an ovule from which a fertile seed was produced. The second loculus was completely sterile.

While it may be argued that such a series as the foregoing is capable of interpretation in either direction, I am inclined to the view that the British species of *Plantago* present a series showing increasing sterilisation in the ovary. It is hoped to extend these observations to include other species of the genus as well as the other genera of the order, when it may be possible to interpret the position with greater certainty.

#### SUMMARY.

A survey of the literature reveals that there is a considerable diversity of opinion as to the structure of the ovary in the genus *Plantago* L.

The British species have been examined in an endeavour to elucidate the structure of the ovary in this genus.

In all five species the ovary is bilocular with an axile placenta, which becomes free at the edges early in development while remaining continuous with the wall of the ovary at the top and bottom of the capsule until this is mature.

In *P. Coronopus* the apparently quadrilocular condition is due to development of placental tissue.

In *P. major* there is a number of ovules and seeds in each loculus of the capsule arranged on the placenta in two tiers. Abortion of some of the ovules is frequent.

In *P. media* there are rarely more than six ovules in the ovary, three in each loculus in two tiers. Several of the ovules usually abort, so that the ripe fruit generally contains fewer than six seeds.

*P. maritima* shows an axile placenta which remains attached to the top of the capsule in two places. In young capsules three ovules were found, two side by side in one loculus and the third at the top of the capsule in the other loculus. Usually two of these ovules abort, giving a mature capsule with one seed.

The bilocular ovary of *P. lanceolata* contains two ovules, of which one is usually abortive, although both ovules may develop. A larger proportion of capsules with two seeds each was found at the top of the inflorescence than at the base.

It is suggested that the British species of *Plantago* present a series showing increasing sterility of the ovary, from the many-seeded condition of *P. major* to the two-seeded condition of *P. lanceolata*, in which a one-seeded fruit frequently results by the abortion of one of the ovules.

The author desires to thank Professor T. G. Hill and Professor E. J. Salisbury for advice and criticism in connection with this work.

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A revision of the genus *Pariana* (Gramineae). By T. G. TUTIN, M.A.

(Communicated by J. RAMSBOTTOM, O.B.E., Sec.L.S.)

(PLATES 8-10, Maps 1 & 2, and 27 Text-figures)

[Read 25 April 1935]

*Historical.*—The genus *Pariana* was first described by Aublet in 'Histoire des Plantes de la Guiane Française', ii, p. 876 (1775), where he defines it as having the male flowers verticillate, the verticils arranged in a spike, and the female flowers solitary in the middle of the surrounding verticil. These essential characters apply without modification to the twenty-three species known to-day, though most of Aublet's other remarks apply to *P. campestris* alone. The figure and description of this, the type-species, agree well with Aublet's specimen in Herb. Mus. Brit., except that the stamens appear to be less numerous in the specimen than in the description, but this is a very variable character in many of the species. The next mention of the genus is in Necker, 'Elementa Botanica', iii, p. 237 (1791), where the name is changed to *Aphonina* for no apparent reason, except possibly because Aublet derived his name from the vernacular instead of from a Greek or Latin source. No new species are described. Palisot de Beauvois does little but repeat this description very briefly in 'Essai d'une nouvelle Agrostographie', p. 121 (1812). Trinius describes a new species and mentions another in Mem. Acad. Petersb., ser. 6, iii, p. 107 (1835), where he gives an account of all the species then known, including those described just previously by Nees in Agrost. Bras. (1829). Miquel gives an account of one new species in 'Linnaea', xix, p. 127 (1847), while Doell, in his account of the genus in Mart. Fl. Bras., ii, pt. 2, p. 338 (1877), describes four more species. He also gives a full description and a figure of the plant that Trinius had mentioned under the name *P. parviflora*, a nomen nudum, but describes it in a new genus *Eremites*, which seems to be merely a section of *Pariana*. Three other species have been described since then by Huber (Bol. Mus. Para, iv, p. 526, 1906), Pilger (Notizbl. Bot. Gaert. Berlin, vi, p. 112, 1914), and Hitchcock (Contrib. U.S. Nat. Herb., xxii, 6, p. 513, 1922), but there has been no complete revision of the genus, though far more collecting has been done in South America in the last few years than ever before.

*Systematic position.*—There are several diverse views about the systematic position of *Pariana*. Trinius placed it in the subfamily Panicoideae (his account was reprinted in a pamphlet entitled 'Panicearum Genera'), and he was followed by Steudel in 'Plantae Glumaceae', i, p. 113 (1855), who placed it between *Spinifex* and *Arundinella*, with neither of which it has any obvious relationship.

Doell suggested that the groups of spikelets might be compared with those of *Hordeum*, and this view was accepted by Hackel in 'Das Pflanzenfamilien', ii, 2, p. 89 (1887), and also by Bews in 'The World's Grasses' (1929). All the evidence for this view will be found in Arber's 'Studies in the Gramineae', vii, pp. 527-31 (Ann. Bot. xliii, 1929). Bentham and Hooker in 'Genera Plantarum', iii, p. 1112 (1883), referred it to the tribe Maydeae, which they made a rather heterogeneous collection of genera. The only reason for considering it to be a member of this tribe appears to be that it has unisexual spikelets, and no other authors have followed this arrangement. Hubbard, in Hutchinson's 'Families of Flowering Plants', ii, p. 219 (1934), has raised Hackel's subtribe of the Hordeae, the Parianeae, to the rank of a tribe, and placed it next to the Phareae. This seems to be the most satisfactory position yet assigned to it, though it is very isolated even here. The Phareae have unisexual spikelets, the female being sessile or shortly pedicelled, and the male having longer pedicels and being smaller. There are also six stamens and sometimes three lodicules, characters which occur in some species of *Pariana*. The resemblance of the inflorescence to that of the Hordeae may well be due to the similarity of conditions during development, and not to any phylogenetic relationship. In facies *Pariana* certainly more nearly resembles the Phareae than any member of the Hordeae and the latter are entirely temperate in their distribution, while the former, like *Pariana*, are entirely tropical. There is no doubt that it is a very isolated genus, and that it belongs in the subfamily Pooideae, not to the Panicoideae in which it was originally placed.

*Generic description*.—Perennial herbs with a creeping or tufted scaly root-stock, giving rise to erect shoots, sometimes woody at the base. In some of the species all culms similar and leafy, in others fertile culms with laminae reduced

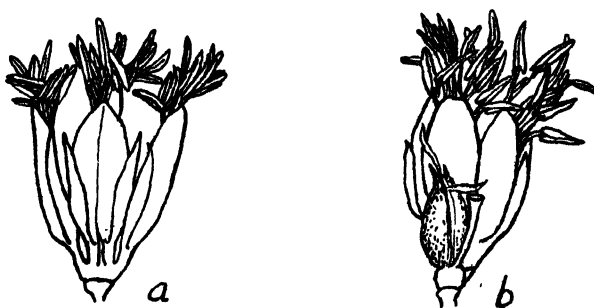


FIG. 1.—a, whorl of spikelets of *P. vulgaris* Tutin; b, with three male spikelets removed to show female spikelet.  $\times 2$ .

till nothing but the sheath remains. Sheaths more or less split, ribbed, puberulent or glabrous, auricled and sometimes fimbriate at the mouth; ligule present, often very short. Petiole short, flattened or caniculate on the upper surface,

lamina broad, ovate to lanceolate, midrib very distinct, lateral veins parallel to it, numerous, a few of them more prominent than the rest, all connected by numerous small veins at right angles to them, pubescent to glabrous, often scabrid on the margin. Leaves often few (sometimes reduced to one) and usually clustered at the top of the culms. Inflorescence a condensed spike-like panicle with the male spikelets on short flattened pedicels in whorls of four to six (usually five), surrounding a solitary sessile female spikelet (figs. 1 & 2). Male spikelets single-flowered, and borne on pedicels usually shorter than the lemma, but sometimes exceeding it. Pedicels hard, flattened, and more or less

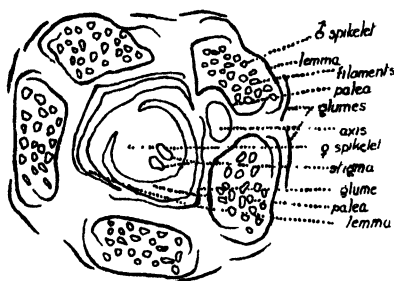


FIG. 2.—Transverse section of whorl of spikelets of *P. vulgaris* Tutin.  $\times 6$ .

fused by one or both margins, most often four of them fused in pairs, and the fifth free, glabrous or pubescent, and often with a well-marked groove or ridge down the middle. Glumes two, lateral, usually shorter than the lemma, one- to three-nerved, rarely with a few small horizontal sinuous veins ('connecting veins') between the main ones, membranaceous or coriaceous, usually more

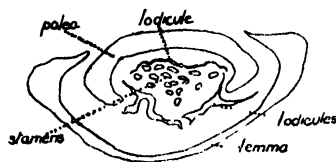


FIG. 3.—Transverse section of male spikelet of *P. campestris* Aubl.  $\times 12$ .  
(Arber, A., Ann. of Bot. xliii, p. 530, 1929.)

or less unequal. Lemma ovate or oblong, rarely lanceolate, obtuse to acute or apiculate, usually glabrous, coriaceous, three- rarely five-nerved, the lateral nerves marginal and often very inconspicuous, connecting veins sometimes present. Palea similar to the lemma, but thinner and often rather shorter, three-nerved, the lateral nerves not marginal, often weak. Stamens usually numerous (few in the *Lanceolatae*), filaments often united into one or more bundles in their lower part, anthers bilocular, hastate at the base, wall of the pollen grain tubercled (fig. 6). Lodicules three, symmetrically arranged in

the *Foliosae* (fig. 3), all abaxial in the *Nudicaules* (fig. 4), usually with a strip of tissue projecting from the back. Female spikelets sessile, not strongly dorsiventral like the male, entirely enclosed by the pedicels of the male (fig. 1 *b*). Glumes two, thin, usually one-nerved, subequal, ovate often acuminate, puberulent or glabrous, more or less enfolding the whole spikelet. Lemma and palea similar, subequal, ovate acute, glabrous or puberulent at the apex, three-

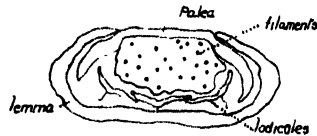


FIG. 4.—Transverse section of male spikelet of *P. vulgaris* Tutin.  $\times 12$ .

nerved, nerves very obscure, strongly indurate, completely enclosing the fruit and falling with it, leaving the glumes behind. Staminodes present in *P. campestris* according to Arber, not observed in any other species. Ovary bluntly trigonous, glabrous, styles two, sometimes partly fused into a tube, stigmas two, feathery. Lodicules three, symmetrically arranged, often large and wrapped round the ovary. Fruit glabrous, bluntly trigonous (fig. 5).

Towards the base and apex of the inflorescence the whorls of spikelets are abnormal, so the descriptions given under the species do not refer to these.

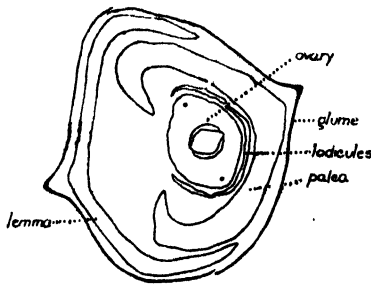


FIG. 5.—Transverse section of female spikelet of *P. vulgaris* Tutin.  $\times 12$ .

The basal whorls have often only four male spikelets, and the female one is sterile or absent, while at the apex there is usually a single spikelet which is female or sterile (the terminal spikelet); this is occasionally accompanied by a few abortive male spikelets. Hitchcock (l.c.) states that there are sometimes two female spikelets in a whorl, but this is not so in any of the specimens examined, nor has any other author recorded it.

*Relationships of the species.*—There is a considerable range of structure in the genus, and the species fall fairly definitely into four sections, which it is proposed to call *Foliosae*, *Lanceolatae*, *Nudicaules*, and *Graciles*. The *Foliosae*

comprises those species which always have the sterile culms and flowering culms similar, the leaves rather broad (at least 2 cm.), and the stamens numerous. In some species the lodicules in the male spikelets are symmetrically arranged round the stamens, and this may apply to all the species, but the limited material available has prevented an examination being made in every case. These characters may perhaps be regarded as primitive for the genus. The *Lanceolatae* is a small and curious section which connects with the *Foliosae*, but shows a great increase in the length of the pedicels of the male spikelets, a reduction in the number of stamens, and often has leafless flowering culms. It corresponds more or less to the genus *Eremites* Doell.

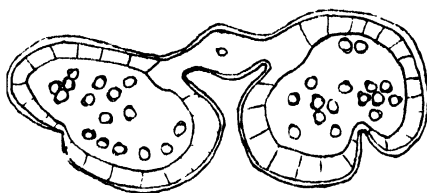
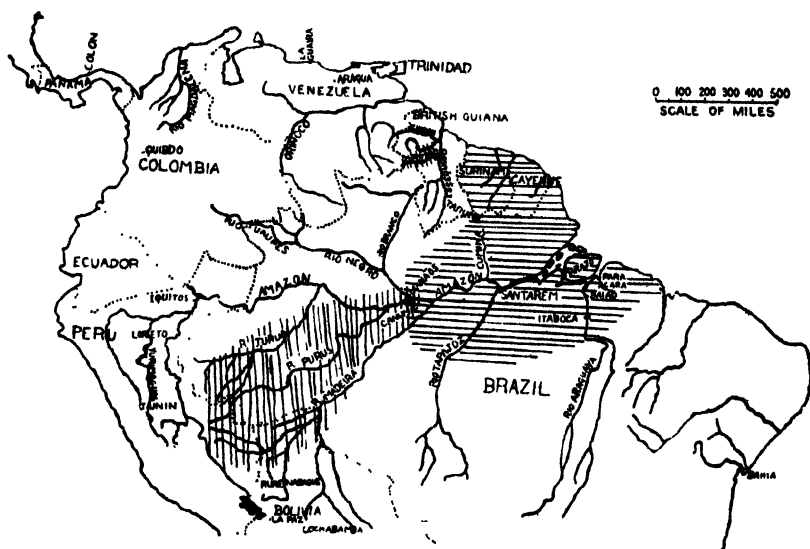


FIG. 6.—Transverse section of anther of *P. vulgaris* Tutin.  $\times c. 50$ .

The next section, *Nudicaules*, has the flowering culms constantly leafless, but the inflorescence stout and the pedicels of the male spikelets short as in the first section. The lodicules in the male spikelets of those species which it has been possible to examine are inserted on the abaxial side of the flower, not symmetrically. The *Graciles* is somewhat similar to the previous section, but there is a reduction in the number of leaves, sometimes to one, the pedicels of the male spikelets are longer, and the inflorescence slender. The lemmas of the male spikelets, leaf-sheaths, and under sides of the leaves are often red or purple, a character which is not found in any of the other sections, but which is rather apt to disappear in herbarium specimens.

*Distribution*.—The genus is confined to the rain forest region of South America, from Panama to Bolivia and Brazil, only two species occurring west of the Andes. The southern limit is rather uncertain, but is at least  $13^{\circ}$  S., while the northern limit is about  $10^{\circ}$  N. Most of the species appear to be very local, but this is probably due partly to insufficient collecting, as the flowers are usually hidden by the leaves and get overlooked. Most of the species are found in rather damp places in low-lying forest, where there is little other herbaceous vegetation, but a few ascend to altitudes up to 5,000 ft. on the eastern slopes of the Andes. The distribution of some of the sections and species is shown approximately on Maps 1 & 2, which also give most of the localities.

*Uses*.—The leaves of *P. trichosticha* ('Canutillo') are used in Colombia for wrapping up gold and platinum dust.



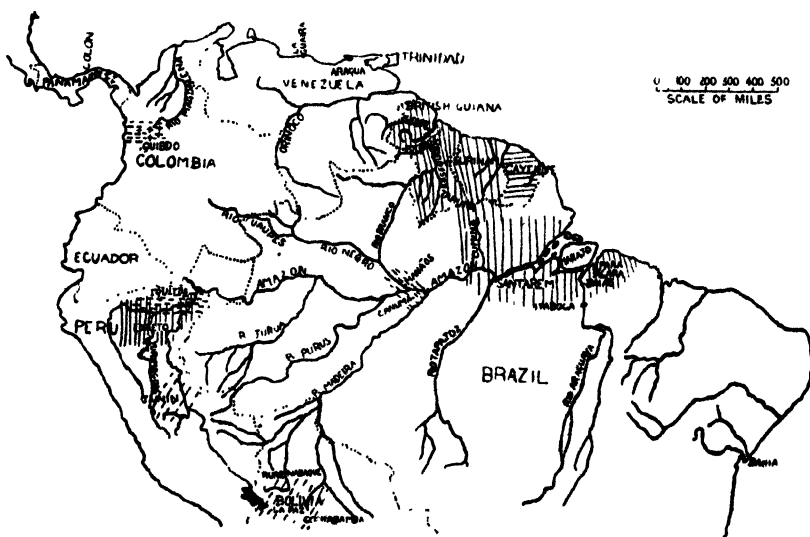
Map. I. Distribution of the Foliosae and Graciles.



Foliosae



Graciles



Map. II. Distribution of six species of the Nudicaules.

*P. radiciflora**P. vulgaris**P. bicolor**P. trichosticha**P. simulans**P. concinna*



My thanks are due to the Director of the Royal Botanic Gardens, Kew, and the Keeper of Botany, British Museum, for obtaining numerous specimens on loan, and to the Keepers of the following Herbaria for lending the specimens in their charge: Berlin, Columbia University, Gray Herbarium, Munich, New York Botanic Garden, Paris, Utrecht, Vienna, and especially to Prof. A. S. Hitchcock for the very numerous specimens at Washington and for photographs. I should also like to thank Messrs. T. A. W. Davis, C. E. Hubbard, and E. F. Warburg for their assistance. My own specimens were collected on the Cambridge Expedition to British Guiana, 1933, and my thanks are specially due to the various bodies who made this expedition possible (see Carter, G. S., J. Linn. Soc. London, Zool., xxxix, p. 148, 1934).

I should also like to thank Mrs. Arber for allowing me to reproduce one of her drawings, and my sister for a number of other drawings.

*Key to the sections and species of Pariana.*

Sections.

- |   |              |
|---|--------------|
| A. Fertile culms leafy and similar to the sterile ones. Leaves at least 2 cm. wide .....  | FOLIOSAE.    |
| B. Fertile culms leafy or leafless. Leaves not more than 1.5 cm. wide.  | LANCEOLATAE. |
| C. Leaves of fertile culms reduced to sheaths, inflorescence stout, pedicels of male spikelets almost hidden .....  | NUDICAULES.  |
| D. Leaves of fertile culms reduced to sheaths, inflorescence slender, pedicels of male spikelets not hidden, sheaths, under sides of leaves, and lemmas often red or purplish ..... | GRACILES.    |

FOLIOSAE.

- |   |                        |
|---|------------------------|
| 1. Male spikelets erect and whorls close, so that the pedicels of one whorl are nearly, or quite, hidden by the lemmas of the whorl below ..... | 2.                     |
| Male spikelets spreading or in rather distant whorls, so that the pedicels of one whorl are not hidden by the lemmas of the whorl below .....   | 3.                     |
| 2. Plant c. 50 cm. high, inflorescence c. 10 cm. long. Lemma less than 6 mm. long .....   | 1. <i>campestris</i> . |
| Plant c. 1 m. high, inflorescence c. 20 cm. long. Lemma 7-8 mm. long .....  | 2. <i>imberbis</i> .   |
| 3. Pedicels of male spikelets nearly as long as the lemma .....   | 5. <i>interrupta</i> . |
| Pedicels of male spikelets up to half as long as the lemma .....  | 4.                     |
| 4. Male spikelets spreading, female in one row, leaves c. 3.5 cm. wide.   | 3. <i>lunata</i> .     |
| Male spikelets erect, female alternate, leaves 2-2.5 cm. wide .....   | 4. <i>intermedia</i> . |

LANCEOLATAE.

- |   |                        |
|---|------------------------|
| 1. Pedicels of male spikelets at least twice as long as the lemma . . . | 2.                     |
| Pedicel and lemma of male spikelets subequal .....                      | 6. <i>tenuis</i> .     |
| 2. Leaves pubescent, stamens 3 .....                                    | 7. <i>lanceolata</i> . |
| Leaves glabrous, scabrid below, stamen 1 .....                          | 8. <i>monothalma</i> . |

## NUDICAULES.

- |  |                           |
|--|---------------------------|
| 1. At least some of the leaves 3.5 cm. wide . . . . .  | 2.                        |
| Leaves not, or scarcely, exceeding 2.5 cm. wide . . . . .  | 9.                        |
| 2. Glumes of male spikelets c. 8 mm. long and terminal spikelet<br>1.5-2.0 cm. long, or leaves at least 30 cm. long. . . . . | 3.                        |
| Glumes not exceeding 6 mm. long, terminal spikelet much smaller,<br>leaves less than 25 cm. long . . . . .                   | 4.                        |
| 3. Leaves 10-15 cm. long, petioles 3 mm. long, ligule very short. . . .  | 14. <i>longiflora</i> .   |
| Leaves 30-35 cm. long, petioles 7-8 mm. long, ligule c. 5 mm. long.  | 10. <i>maynensis</i> .    |
| 4. Glumes c. 2 mm. long, or very broad in proportion to their length.  | 5.                        |
| Glumes c. 4 mm. long, at least one subulate or almost setaceous. . .   | 7.                        |
| 5. Midrib conspicuously tomentose above . . . . .  | 16. <i>trichosticha</i> . |
| Midrib glabrous or puberulent above. . . . .   | 6.                        |
| 6. Leaves glaucous below, whorls of spikelets usually rather distant.  | 15. <i>bicolor</i> .      |
| Leaves not glaucous, whorls of spikelets close together. . . . .   | 11. <i>radiciflora</i> .  |
| 7. Glumes decurrent, very unequal, pedicles winged at least on one<br>side . . . . .   | 12. <i>Ulei</i> .         |
| Glumes not, or scarcely, decurrent. . . . .  | 8.                        |
| 8. Lemma narrowly lanceolate, scaberulous, glumes narrow, con-<br>necting veins absent . . . . .                             | 9. <i>stenolemma</i> .    |
| Lemma ovate to oblong, abruptly acute, smooth, glumes usually<br>broader, connecting veins often present . . . . .           | 13. <i>vulgaris</i> .     |
| 9. Glumes 2-3-nerved, membranaceous, sheaths scarcely auricled . .   | 10.                       |
| Glumes coriaceous, at least one with a single prominent nerve,<br>sheaths strongly auricled . . . . .                        | 17. <i>zingiberina</i> .  |
| 10. Glumes triangular, long acuminate, ciliate . . . . .   | 18. <i>simulans</i> .     |
| Glumes subulate, glabrous . . . . .  | 19. <i>concinna</i> .     |

## GRACILES.

- |  |                          |
|--|--------------------------|
| 1. Leaves about 25 cm. long, 6 cm. wide, solitary or rarely two. . . . | 22. <i>Gleasoni</i> .    |
| Leaves smaller, two or more . . . . .                                  | 2.                       |
| 2. Spikelets often 4 in a whorl, glumes obtuse . . . . .               | 23. <i>debilis</i> .     |
| Spikelets 5 in a whorl, glumes acute . . . . .                         | 3.                       |
| 3. Lemma acute, pedicel often pubescent all over, 2.5-3 mm. long . .   | 20. <i>gracilis</i> .    |
| Lemma obtuse, pedicel bearded at the base, c. 4.0 mm. long . . . .     | 21. <i>pulcherrima</i> . |

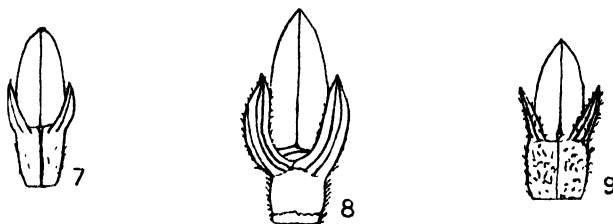
## FOLIOSAE.

1. *PARIANA CAMPESTRIS* Aubl. Hist. Plant. Guiane Française, ii, p. 876, t. 237 (1775).

*Pariana glauca* Nees, Agrost. Bras. (1829) ; *P. scabra* Nees, l.c. ; *P. silvestris* Nees, l.c. ; *P. inaequalis* Miq. Linnaea, xix, p. 127 (1847).

Culms about 50 cm. high, closely covered by the imbricating sheaths, which may be glabrous or puberulent between the ribs and nearly invariably have abundant spreading fimbriae at the mouth. Leaves shortly petioled, lanceolate or ovate to oblong cuspidate, and more or less rounded at the base, 10-25 cm. long and 3-5 cm. wide, glabrous and smooth, or scabrid, above, pubescent, scabrid, or smooth below. Ligule very short, truncate. Inflorescence 10-

12 cm. long, 0.8–1.0 cm. wide, whorls of male spikelets close together, pedicels short; lemma 4–6 mm. long, glabrous or pubescent, acute to rather obtuse, glumes from 0.25–0.75 the length of the lemma, usually narrow and 1–2-nerved, rarely broader and 2–3-nerved (fig. 7), stamens about 20, filaments more or less fused at the base; lodicules 3, ciliate. Female spikelet solitary in each whorl of five male spikelets. Glumes 6–7 mm. long, ovate acuminate, puberulent, 1-nerved, and somewhat keeled; lemma 5.5–6.0 mm. long, palea slightly shorter, both acute, glabrous except for the apex, which is sparsely puberulent, strongly indurate, even before flowering, and wrapped round the fruit. Lodicules 3,



FIGS. 7–9.—Male spikelets,  $\times 2.5$ . 7. *P. campestris* Aubl., from type-specimen. 8. *P. imberbis* Nees, from Killip & Smith, 30487. 9. *P. lunata* Nees, from Spruce, s.n., in Herb. Kew.

ovate, one 1.0 mm. long, the others 1.5 mm. long, the two larger with a small pouch on the inner side. Style flat, 1.5 mm. long, stigmas 2 rather broad, fimbriate; ovary glabrous, 2 mm. long. Terminal, spikelet, female about 8 mm. long.

*Distribution*.—BRAZIL, Prov. of Para; CAYENNE; SURINAM. Type in Herb. Mus. Brit.: Cayenne, Aublet s.n.

This is a very variable species, the extreme forms differing considerably from one another in appearance, but being connected by every intermediate. The various forms are not confined to particular localities nor do the intermediates appear to be rare, so that there is no evidence at present for the existence of several races or subspecies. The species given above as synonyms were described on scanty material, and Doell in Mart. Fl. Bras. suggested that they were probably not distinct. The much more abundant material now available (particularly that in the U.S. National Herbarium) confirms this. The following are the main points of difference between these 'species':—*P. glauca*: leaves thick, glaucous, fairly broad at the base, cuspidate, smooth. *P. scabra*: leaves thick, glaucous, longer and narrower, acuminate, scabrid on the margins. *P. silvestris*: leaves thin, bright green, very broad at the base, cuspidate, smooth. *P. inaequalis*: leaves ovate-lanceolate, acuminate, unequal at the base, pedicels of the male spikelets pubescent.

The type-specimen has ovate cuspidate leaves, and the pedicels of the male spikelets are ciliate on the margins, but otherwise glabrous. Vernacular name in Cayenne : ' *Pariane* '—Aublet.

2. *PARIANA IMBERBIS* Nees, *Agrost. Brasil.* p. 297 (1829).

Culms stout, 1 m. or more high, leaves less crowded than in *P. campestris*, but sheaths imbricate, strongly ribbed, glabrous or with short sparse hairs on the sides of the ribs, fimbriae at the mouth of the sheath not very abundant or sometimes absent. Leaves shortly petioled, lanceolate, acuminate or cuspidate, rounded and very unequal at the base, 20–27 cm. long, 4·5–6·0 cm. broad, smooth or nearly so above, scabrid or pubescent below. Ligule about 2 mm. long. Inflorescence about 20 cm. long, 1·0–1·5 cm. wide, whorls of male spikelets close together, pedicels about 3 mm. long; lemma 7–8 mm. long, oblong, apiculate or acute, glumes broad, smooth, 2–3-nerved, ciliate (fig. 8). Glumes of the female spikelet 7–8 mm. long, ovate acuminate, 3-nerved, sparsely puberulent; lemma 6 mm. long, ovate, 3-nerved, with a slight keel at each nerve, glabrous except at the apex, which is puberulent; palea without visible nerves, folded round the fruit, otherwise similar to the lemma. Lodicules 3, cuneate. Fruit 3·0–4·5 mm. long, bluntly trigonous. (Pl. 8.)

*Distribution*.—BRAZIL, Prov. of Para, Martius, *Iter Bras. Herb. Munich*, 12572 & 12574; Burchell 9265 at Baião, *Herb. Kew.* Goldei 9, Mojú River, 'in forest on sandy loamy soil'. Goldei 307 bis, Bragança railway. Killip and Smith 30487, Ilaha do Mosqueiro. U.S. Nat. Herb. Prov. of Amazonas, Martius s.n., Manãos, Rio Negro. Type, *Herb. Munich*, 12569.

Rather similar to *P. campestris*, but no intermediate forms seem to occur. Apparently it is confined to the lower Amazon valley. It may be distinguished by the greater size of all its parts and by the glumes and lemmas of the male spikelets being generally dark brown, instead of straw-coloured as is usual in *P. campestris*.

3. *PARIANA LUNATA* Nees, *Agrost. Bras.* p. 295 (1829).

*Pariana mollis* Nees, *Agrost. Bras.* p. 296.

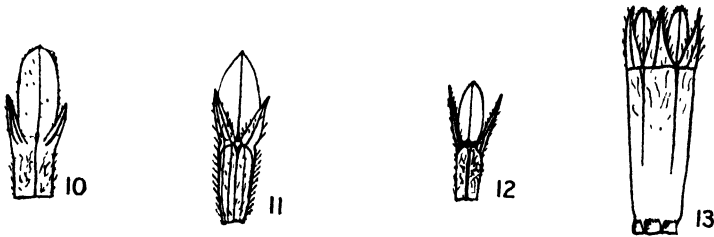
Culms about 60 cm. high, and 3–4 mm. thick, leaf-sheaths imbricate, strongly ribbed, glabrous or with short sparse hairs on the sides of the ribs, fimbriae not very abundant, sometimes absent. Leaves lanceolate, acuminate, scabrid or pubescent below, scabrid above, 15–25 cm. long, and 4–5 cm. broad. Ligule often as much as 5 mm. long. Inflorescence 12–14 cm. long, 1·2–1·5 cm. wide, whorls of male spikelets rather distant, spikelets spreading, pedicels about 3 mm. long, pubescent, fused in pairs; lemma 5–6 mm. long, ovate-oblong, acute, glumes narrow-triangular, acute, 1–2-nerved, ciliate, 0·3–0·5 the length of the lemma (fig. 9). Stamens about 12, free. Lodicules 3, about 0·5 mm. long, flabellate. Female spikelets in a single row on the axis, not alternate as in most species. Glumes about 7 mm. long, fruit 5 mm. long.

*Distribution*.—BRAZIL, Prov. of Para, Martius, Herb. Munich 12571 & 12573 ; Spruce, s.n., Herb. Kew. ; Goldei 88, Marjo Island, Karakara River, and 307 Bragança railway ; Mexia 6052 a, Rio Acara, U.S. Nat. Herb.

The name *P. mollis* Nees seems to refer to this species when the leaves are pubescent below, instead of scabrid. I can find no other difference.

4. *PARIANA INTERMEDIA* Doell in Mart. Fl. Bras. ii, pt. 2, p. 337 (1877).

Culms 30–40 cm. high, sterile ones about 2 mm. in diameter and rather woody, fertile culms usually stouter and softer, sheaths, except the lowest, puberulent, strongly imbricate, fimbriae usually present, spreading. Leaves 6–11 cm. long, 2.0–2.5 cm. wide, lanceolate, acuminate, smooth above, scabrid and glaucous below ; petioles 2–3 mm. long, pubescent. Ligule 2–3 mm. long, about 1 mm. long, truncate. Inflorescence sometimes borne on a nearly leafless



FIGS. 10–13.—Male spikelets,  $\times 2.5$ . 10. *P. intermedia* Doell., from Spruce 876 in Herb. Kew. 11. *P. interrupta* Tutin, from type-specimen. 12. *P. tenuis* Tutin, from type-specimen. 13. *P. lanceolata* Trin., from cotype in Herb. Kew.

stem, 8–10 cm. long, 7–9 mm. thick, whorls of male spikelets rather distant, spikelets somewhat spreading, pedicels 3 mm. long, pubescent, one pair fused by one margin ; lemma 3.5–5.0 mm. long, ovate-acute, puberulent, glumes 0.3–0.5 the length of the lemma, 1–2-nerved, subulate, somewhat obtuse, ciliate on the margins (fig. 10). Stamens about 10, usually fused in two groups with two or three free ones. Glumes of the female spikelet 7 mm. long, oblong-lanceolate, acute, 1-nerved, puberulent at the apex, lemma and palea 6 mm. long, ovate, glabrous. Lodicules 2 mm. long, wrapping round the ovary. Ovary 3 mm. long, with 2 nearly distinct styles and long plumose stigmas. Terminal spikelet sterile.

*Distribution*.—BRAZIL, Prov. of Para, Spruce 855, Santarem, Herb. Munich. Type, Spruce 876 and s.n. Santarem, Herb. Kew., N.Y. Bot. Gard., Univ. Cantab., Mus. Palat. Vindob.

5. *PARIANA INTERRUPTA* Tutin, sp. nov.*Pariana nivea* Huber MS., *nomen*.

A speciebus aliis seriei pedicellis longis, lemmate spicularum mascolarum breve, verticillis spicularum mascolarum distantissimis praesertim versus basim inflorescentiae differt.

*Herba* perennis plus minusve lignosa, 1 m. alta, vaginis glabris vel puberulis, raro fimbriatis; ligula brevissima. *Folia* 10–20 cm. longa, 3–4 cm. lata, lanceolata, acuminata supra glabra, subtus scabrida, et plus minusve glauca. *Inflorescentia* 8–10 cm. longa, 6–7 mm. lata, a vagina superiore longe exserta. *Spiculae masculae* 5 in verticillis omnibus paribus junctis, verticillis distantibus ut inflorescentia interrupta videatur praesertim versus basim; pedicelli 3–5 mm. longi pilis appressis, sericeis vestiti; glumae 2–3 mm. longae saepissime satis robustae; lemma 3–4 mm. longum, elliptico-lanceolatum, glabrum, costa satis prominente, nervis marginalibus obsoletis, connectentibus nullis; palea lemmati similis, obsolete quinquenervis, satis indurata (fig. 11). *Spiculae feminae* uniseriatae; glumae ovatae, acutae 7 mm. longae, ciliatae, parum carinatae; lemma paleaque 6 mm. longae, glabrae.

*Distribution*.—BRAZIL, Prov. Rio Negro, Spruce s.n., prope Barra (Manãos) 1855, typus in Herb. Kew. Manãos 1910, Ule 8815. Prov. of Para, Burchell 9194, Itaboca, 1829. Spruce, s.n., in silvis fluvii, Taruma, Feb. 1852, Herb. Kew. This locality appears to be near the boundary of Brazil and British Guiana, so this species may perhaps be found in the southern part of Guiana when this is explored more thoroughly. COLOMBIA, Spruce 2749 in silvis fluvii Uaupés, Oct. 1852, Herb. Kew.

The very long hard pedicels found sometimes in the male spikelets of this species suggest a relationship with the next section (*Lanceolatae*), and are also similar to those of *P. bicolor*, a member of the *Nudicaules*. The peculiarity of having the female spikelets in a single row is shared with *P. lunata*, but the present species may be readily distinguished from all others in this section by the distant whorls of male spikelets, and by the lemma being about equal in length to the pedicel.

## LANCEOLATAE.

6. *PARIANA TENUIS* Tutin, sp. nov.

A speciebus aliis seriei inflorescentia tenuissima, lemmate spicularum mascolarum pedicellum subaequante, staminibus 6, differt.

*Herba* perennis caespitosa. *Culmi steriles* 25–30 cm. alti, vaginae glabrae, superiores densae, foliatae, inferiores, 2 vel 3, distantes, aphyllae. *Folia* 7–12 cm. longa, 0.7–1.2 cm. lata, linearia, acuta, supra glabra, subtus plus minusve scabrida; petioli c. 1 mm. longi, glabrescentes. *Culmi floriferi* c. 15 cm. alti tenues, vaginis quam internodiis brevioribus, vix inflatis. *Inflorescentia*

3.5 longa, 0.5–0.6 cm. lata. *Spiculae masculae* 5 in verticellis omnibus, paribus junctis ; pedicelli 3 mm. longi, pubescentes ; glumae 2.5–3.0 mm. longae, angustissimae, uninerves, ciliatae, acutae ; lemma 3 mm. longum, lanceolatum, acutum, nervibus satis obsoletis ; palea lemma aequans ; stamina 6 ; lodiculi parvi (fig. 12). *Spiculae feminae* uniseriatae ; glumae 4 mm. longae, anguste, lanceolatae, acutae, carinatae, ciliolatae ; lemma paleaque 4 mm. longae, ovatae, acutae, apice minute pubescentes. *Spicula terminalis* sterilis.

*Distribution*.—COLOMBIA or BRAZIL. In fluviis Uaupés inundatis, Spruce 2919, typus in Herb. Kew.

This species resembles *P. interrupta* in having the pedicel and lemma of the male spikelet subequal, but differs from it in its smaller size, narrower leaves, and different shape and size of the glumes. The only locality given by Spruce is Rio Uaupés, so it is impossible to say whether it was found in Colombia or Brazil. A number of interesting plants were found by Spruce in this district, and it seems well worth further investigation.

7. *PARIANA LANCEOLATA* Trin. in Mem. Acad. Petersb. ser. 6, iii, p. 107 (1835) (*Panicearum Genera*, 19).

Culms about 25 cm. high, slender, all leafy, sheaths ciliate at the margins, fimbriae rather spreading, few. Leaves linear-lanceolate, pubescent on both surfaces. Inflorescence small, cylindrical and compact, 4 mm. thick ; pedicels of male spikelets 8–10 mm. long, sparsely pubescent, fused in pairs ; lemma 2 mm. long, equalling the glumes, ciliate ; glumes elliptical to ovate, with an outward curving point, 3-nerved, pubescent, one or more pairs fused (fig. 13) ; stamens three ; lodicules nearly equalling the filaments, c. 2 mm. long. Female spikelets 8–10 mm. long. acute, lemma and palea c. 9 mm. long, lanceolate, two-keeled, closely wrapped round the ovary, terminated by a small point which is slightly expanded distally ; ovary c. 5 mm. long, lodicules 3, 1 mm. long. (Pl. 8.)

*Distribution*.—BRAZIL, Bahia, Riedel. Type in Herb. Hort. Petrop.

A duplicate of the type-specimen in Herb. Kew. is the only one seen. No further information about the locality is given on Riedel's label.

8. *PARIANA MONOTHALMA* (Doell) Tutin, comb. nov.

*Eremites monothalma* Doell. Fl. Bras. ii, pt. 2, p. 338 (1877).

Culms compressed, sterile leafy, fertile leafy, or leafless, nodes more or less hairy. The sheaths of the leaves striate, nerved, ciliate on the margin, fimbriae long, upper sheaths somewhat inflated ; ligule very short, truncate, ciliolate. Leaves shortly petiolate, lanceolate from a broad base, or narrowly subobovate-lanceolate, acuminate, sparsely hairy above, scabrous on the margin, slightly scabrous below. Inflorescence similar to that of the previous species ; pedicels of male spikelets fused into two semitubular sheets, c. 1.4 cm. long ; lemma

oblong-linear, about equalling the glumes, much shorter than the pedicel; glumes subulate-lanceolate; stamen one. Glumes of the female spikelet linear-subulate, 1-nerved; lemma and palea indurate, convolute-subtubular, oblong-lanceolate, acuminate, exceeding the glumes.

*Distribution*.—BRAZIL, Bahia. Riedel. Type in Herb. Hort. Petrop.

The above description is based on Doell's account and figure in 'Flora Brasiliensis', since it was impossible to obtain the type-specimen on loan, and there do not appear to be any other specimens in herbaria. Trinius's original description of *P. parviflora* (Mem. Acad. Petersb. ser. 6, iii, p. 105, 1835) is as follows: 'In specie Bahiensi quadam (*P. parviflora* Herb. nostr.) incompleta, laciniae istae fere ex ipsa articuli basi nascuntur, stipite subnullo'. The chief point of interest in it is that the specimen is described as being incomplete, a point which Doell overlooks when he uses the small number of flowers as a character of his genus *Eremites*.

Since this is all the description that Trinius gives, and he obviously had no intention of describing the species then, the name *P. parviflora* is a nomen nudum, and Doell's description in the genus *Eremites* is the valid one. *Anomochloa marantoidea* Brongn. has the same locality 'Bahia' without further details, and Mrs. Chase, in a letter to Mrs. Arber, suggests that it is possible that this refers to Bahía de Rio de Janeiro, and not to Bahia de Todos os Santos. The former is about 23° S., while the latter is about 13° S., and hence seems the more probable locality. Whichever locality is correct, it represents the southern limit of the genus as at present known.

## NUDICAULES.

### 9. *PARIANA STENOLEMMA* Tutin, sp. nov.

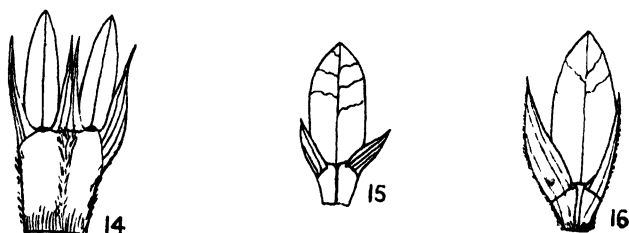
*P. vulgari* affinis sed statura majore, foliis magis numerosis, nodis barbatis, glumis angustis, lemmatibus anguste lanceolatis scaberulis.

*Herba* perennis. *Culmi* steriles usque 2 m. alti, vaginis imbricatis plerumque 12 vel pluribus foliatis, saepissime ad orem fimbriis paucis erectis praeditis. *Folia* 14–25 cm. longa, 2.5–5.5 cm. lata, lanceolata, vel elliptico-lanceolata, acuminata, utrinque glabra; petioli 2–4 mm. longi, plus minusve pubescentes.

*Inflorescentia* 8–10 cm. longa, c. 1 cm. lata. *Culmi* floriferi c. 30 cm. alti, vaginis paulum inflatis, glabris, inter costas saepe scabridis. *Spiculae masculae* 5 in verticillis omnibus paribus junctis; pedicellis 3.0–3.5 mm. longis, basi pubescentibus; glumae 5–6 mm. longae, subulatae, acutae, 2- vel 3-nerves, scabridae; lemma 6–7 mm. longum, anguste lanceolatum, acutum, costa satis prominente, nervis obsoletis; palea anguste, obtusa, quinquenervis; stamina c. 15 antheris valde hastatis, filamentis libris; lodiculae 0.25–0.5 mm. longae, oblongae (fig. 14). *Spiculae feminae* uniseriatae; glumae 8 mm. longae, ovatae, acutae, carinatae, glabrae; lemma paleae ovatae, acutae, 6–7 mm. longae. *Spicula terminalis* femina vel sterilis et spiculis masculis 1 vel 2 comitata.



*Distribution*.—PERU, Dept. Loreto, Mishuyacu, near Iquitos, altitude 100 m. in forest. G. King 956, Feb.–March 1930. Type in U.S. Nat. Herb., duplicate in Herb. N.Y. Bot. Gard. Dept. Loreto, Pinto-Cocha on the Rio Nanay, Llewelyn Williams 787, June 1929 U.S. Nat. Herb.



FIGS. 14–16.—Male spikelets,  $\times 2.5$ . 14. *P. stenolemma* Tutin, from type-specimen. 15. *P. radiciflora* Sagot, from cotype in Herb. Kew. 16. *P. Ulei* Pilger, from cotype in Herb. Kew.

BRAZIL, ‘in silviis fl. Uaupés’, Spruce 2819 in Herb. Kew.

VENEZUELA, rain forest on road Maracay–Ocumare, Aragua, Aug. 1925, H. Pittier 11852. U.S. Nat. Herb.

The large size, very numerous leaves, and narrow lemmas tapering upwards from near the base make this plant readily recognisable.

#### 10. *PARIANA MAYNENSIS* Huber in Bol. Mus. Para, iv, p. 526 (1906).

Sterile culms 1 m. or more high, 5 mm. thick, swollen at the nodes, lightly pubescent; the lower 3 or 4 with very reduced leaves, the upper ones with large leaves, fimbriae absent. Leaves c. 30–35 cm. long, 6–9 cm. wide, acutely acuminate, scabrid on the margin, glaucescent below, petiole 7–8 mm. long. Ligule c. 5 mm. long. Fertile culms 30–40 cm. high, sheaths somewhat inflated, nearly or quite leafless, shorter than the internodes. Inflorescence 10 cm. long, rhachis fragile; pedicels of the male spikelets pilose at the base; glumes subulate-lanceolate or almost setaceous, 2-nerved, twice as long as the pedicel, and scarcely exceeded by the lemma. Lemma lanceolate-acute, midrib prominent, lateral veins and connecting veins inconspicuous. Female spikelets with glumes 7 mm. long, 1-nerved, keeled, glabrous, ovate-acuminate; lemma and palea 6 mm. long, glabrous, ovate-acute.

*Distribution*.—PERU, Loreto, Cerro de Canchahuaya, November 1898, J. Huber. Type probably in Herb. Mus. Para.

SURINAM, in silva prope Wonotobo, Corantyn, October 1916, 2533 in Herb. Utrecht. ‘1 m. high, flowers brown-green. Vern. nom. Tamakoesji, Kar.’

I have been unable to examine the type-specimen of this species, and, as the description is not very detailed, the Surinam specimen is referred doubtfully to it. From the point of view of geographical distribution, it seems unlikely

that the two are identical, but Huber's description fits it well, and it is certainly distinct from all the other species. *P. maynensis* is placed next to *P. stenolemmu* on account of the long narrow glumes about equalling the lemma, and the large size of the leaves and culms.

11. *PARIANA RADICIFLORA* Sagot ex Doell. in Mart. Fl. Bras. ii, pt. 2, p. 336 (1877).

Sterile culms c. 30 cm. high, sheaths puberulent or glabrous, the lower ones usually leafless, fimbriae present or rarely absent. Leaves 10–12 cm. long, 3–5 cm. wide, elliptic, acute, smooth on both sides. Ligule very short, truncate. Fertile culms c. 15 cm. high, softer than the sterile ones. Inflorescence erect, rather stout, pedicels of male spikelets 2–2.5 mm. long; lemma 5 mm. long, broadly elliptic-oblong, midrib, marginal nerves, and horizontal connecting nerves rather prominent; glumes c. 2.5 mm. long, acute, one 3-nerved, the other 2-nerved (fig. 15); stamens c. 20, filaments free. Glumes of the female spikelet 5.5 mm. long, ciliate on the keel and margins, shortly pubescent at the tip. Lemma and palea 5 mm. long. Ovary 2 mm. long; lodicules 1 mm. long, narrowly oblong.

*Distribution*.—CAYENNE (French Guiana), Sagot 701. Type in Herb. Paris. Duplicates in Herb. Mus. Brit., Herb. Kew., Herb. Univ. Cantab., etc.

This species was the first of this group to be described, and a large number of specimens have been placed under it in herbaria. Several sheets of the type-collection have been examined, and they are all of them constantly distinct from other collections to which they bear a superficial resemblance. *P. Ulei* and *P. vulgaris* are most liable to be confused with the present species, but the points of difference, though small, are numerous and constant. The former may be distinguished by the much longer, unequal glumes of the male spikelets, which are decurrent on the pedicel, and the latter by the longer, narrower single-nerved glumes, and larger leaves and stems.

12. *PARIANA ULEI* Pilger in Notizbl. Bot. Gaert. Berlin, vi, p. 112 (1914).

Sterile culms rather woody, sheaths glabrous, fimbriae few or none. Leaves lanceolate-acuminate, scabrid on the margin, otherwise smooth. Ligule very short. Upper sheaths of fertile culms sometimes with a small erect or reflexed lamina; pedicels of male spikelets about 3 mm. long, pubescent at the base; lemma 6–7 mm. long, oblong, acute, glabrous, midrib prominent, margins somewhat thickened; glumes 3.5–4.0 mm. long, one 3-nerved, the other 1-nerved, decurrent on the pedicel, giving it a winged appearance (fig. 16). Stamens about 20, filaments fused in the basal half. Male spikelets six in each whorl, their pedicels fused in pairs. Female spikelets solitary in each whorl of male spikelets, first glume 8 mm. long, narrowly lanceolate, acute, keeled, 1-nerved, puberulent; second glume 7 mm. long, oblong-lanceolate, acute, scarcely keeled, with one rather weak excentric nerve, puberulent; lemma and palea 5 mm. long, ovate, rather abruptly acute, scaberulous at the apex.

Lodicules 1 mm. long, or slightly less, orbicular, crenate undulate. Ovary 1.5 mm. long, glabrous, styles 2, rather thick and very short, stigmas 2, 6 mm. long, with threads c. 2 mm. long.

*Distribution*.—BRAZIL, Rio Juruá, Oct. 1900. Ule 5307. Type in Herb. Berlin. Duplicate in Herb. Kew.

Lower Amazons, Trail 1265. Herb. Kew.

COLOMBIA, New Granada, André 1107. Herb. Kew.

The occurrence of six male spikelets in a whorl is probably the most striking thing about this species, as the number is so constantly five in the genus as a whole. The long feathery stigmas are of the usual grass type, but appear to be better developed in this species than in the other members of the genus.

### 13. *PARIANA VULGARIS* Tutin, sp. nov.

Affinis *P. radiciflora* Sagot quae foliis minoribus, latioribus, fimbriis pluribus, glumis brevioribus, magis patentibus, bi- vel trinerviis, spicula femina minore, differt.

*Herba* perennis, caespitosa, stolonifera. *Culmi* steriles 40–60 cm. alti; vaginae inferiores quam internodi breviores, plus minusve puberulae, ore paulum auriculatae, fimbriis nullis vel paucis brevibusque, superiores 4–8 foliatae. *Folia* acuta, lanceolata, usque elliptica, 10–18 cm. longa, 3–4.5 cm. lata, levia, petiolis 3–4 mm. longis, puberulis. *Culmi floriferi* crassi, 25–30 cm. alti; vaginae quam internodi saepissime breviores, valde inflatae, superiores glabrae, inferiores non nunquam minute puberuli. *Inflorescentia* 5–6 cm. longa, crassa, vagina superiore ad basin attingente. *Spiculae masculae* 5 in verticillis; pedicellis 2 mm. longis, glabris, paribus fuis, quinta spiculare feminae opposita; glumae 5–6 mm. longae, subulatae, uni- vel bi-nerves, glabrae, utrinque 3–5 nervis sinuosis horizontalibus instructum; lemma 6–7 mm. longum, oblongo-ellipticum, acutum, uninerve, utrinque 3–5 nervis sinuosis horizontalibus instructum; palea lemma subaequans; stamina circa 20 (fig. 17). *Spiculae feminae* alternatae; gluma prima 9 mm. longa, uninervis, valde carinata, glabra, marginibus ciliata, lanceolata, acuta; gluma secunda 8 mm. longa, uninervis, carinata, marginibus ciliata, triangularis, apice seta praedita; lemma paleaque ovata, acuta, 6–6.5 mm. longa, glabra, apice excluso; lodiculi 1.5 mm. longi, 0.6 mm. lati, oblongi, truncati; ovarium 3.5 mm. longum, glabrum, satis tenue, stigmatibus compressis, membraneis, pubescentibus. *Spicula terminalis* femina 7–8 mm. longa. *Fructus* 3.5 mm. longus, 2.5 mm. latus.

*Distribution*.—BRITISH GUIANA, near a branch of Waiapi Creek, Cuyuni River, Tutin 38. Typus in Herb. Mus. Brit.

By far the commonest species in British Guiana. SURINAM. To be expected in Cayenne.

BRAZIL, Prov. of Para, Schwacke 43, collection 3. U.S. Nat. Herb. and N.Y. Bot. Gard. Rio Cumina, Sampaio 5165. U.S. Nat. Herb.

PERU, Dept. Loreto, Killip and Smith, 27009. N.Y. Bot. Gard. and U.S. Nat. Herb. Llewelyn Williams, 4098. Same loc., U.S. Nat. Herb.

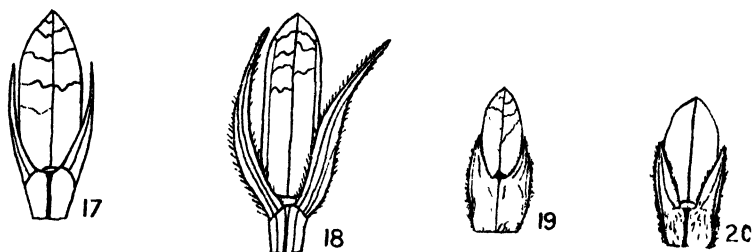
There is one specimen in Herb. Kew. which is said to come from St. Vincent, West Indies, but in the absence of any other record it seems best to regard this with suspicion. No other species is recorded from the West Indies, though they might be expected to occur, particularly in Trinidad, which has a more continental flora than the other Islands.

*P. vulgaris* is recorded under the name of *P. radiciflora* Sagot in Hitchcock, 'Grasses of British Guiana' (Contrib. U.S. Nat. Herb. xxii, pt. 6, 1922). Vernacular names (Surinam): *Léroé basambéroé* (Arawak) and *Tamakoeji* (Kar.).

14. *PARIANA LONGIFLORA* Tutin, sp. nov.

Ab aliis speciebus seriei spiculis magnis, glumis spiculæ feminae quinque-nervibus, facile distinguitur.

*Herba* perennis, robusta, repens, caespes formans. *Culmi steriles* 40–60 cm. alti; vaginae inferiores aphyllae vel raro lamina parva praedita, raro imbricatae,



FIGS. 17–20.—Male spikelets,  $\times 2.5$ . 17. *P. vulgaris* Tutin, from type-specimen. 18. *P. longiflora* Tutin, from type-specimen. 19. *P. bicolor* Tutin, from type-specimen. 20. *P. trichosticha* Tutin, from type-specimen.

non inflatae, pubescentes, ori auriculatae et saepissime fimbriis parvis instructae; vaginae superiores imbricatae, foliatae. *Folia* glauca, ovato-lanceolata, acuta, 10–15 cm. longa, 3–4 cm. lata, saepissime prope basin latissima, petiolis 3 mm. longis, pubescentibus. *Culmi floriferi* robusti, 40–50 cm. alti; vaginae quam internodii saepissime breviores, superiores valde inflatae. *Inflorescentia* circa 10 cm. longa, robustissima, sub anthesi basi ab vagina superiore plus minusve inclusa. *Spiculae masculae* 5 in verticillis; pedicellis 2 mm. longis, marginibus ciliatis, paribus fuis, quinta spiculæ feminae opposita; glumae 8–9 mm. longae, bi- vel trinerves, subulatae, ciliatae; lemma 9–10 mm. longae, trinerve utrinque 3–4 nervis sinuosis horizontalibus instructum, oblongum acutum; palea lemma subaequans; stamina circa 18 (fig. 18). *Spiculae feminae* alternatae; glumae 12–13 mm. longae, anguste lanceolatae, acutae, puberulae, quinquenerves, costa forte, nervis lateralibus minus prominentibus ad apicem non attingentibus, nervis marginalibus satis obsoletis; lemma 8 mm. longum, acutum, obsolete paucinerve, paleam ex toto involvens, angulis puberulum; palea 8 mm. longa,

acuta, glabra, sine nervis, marginibus involutis; lodiculi 1 mm. longi, apice ciliati; ovarium glabrum, stylo breve, crasso, ramis duobus membranaceis, compressis, instructo c. 6 mm. longo, superne longe tenueque hirsuto. *Spicula terminalis* c. 1.5–2.0 cm. longa, femina; glumae acutae, saepissime tortae, lemma multo superantes.

*Distribution*.—BRITISH GUIANA, Karau Creek, Mazaruni Station, in Mora forest. Tutin 39. Typus in Herb. Mus. Brit.

This species is probably most closely allied to *P. vulgaris*, but is readily distinguished from it by the very large size of the spikelets, particularly the terminal one, and by the five-nerved glumes of the female spikelet. The plant from which the specimens were obtained was the only one seen, and formed a large patch in a swampy hollow, near the creek. It was in full flower at the beginning of May 1933, and continued to flower during the greater part of the following three months. The flowering culms were hidden by the taller sterile culms, as in most of the species of this genus, and this has probably given rise to the impression that these forest grasses seldom flower.

#### 15. *PARIANA BICOLOR* Tutin, sp. nov.

Affinis *P. radiciflorae* Sagot a qua foliis subtus glaucis, verticillis spicularum masularum satis distantibus, pedicellis saepe albis conspicisque, lemmate glumisque crassis differt.

*Herba* perennis. *Culmi steriles* usque 80 cm. alti, vaginis imbricatis, superioribus paucis foliatis. *Folia* 12–22 cm. longa, 2.5–5.0 cm. lata, oblonga vel ovata, acuminata, subtus saepissime scabrida et glauca; petioli 2–3 mm. longi, puberuli. *Inflorescentia* 7–9 cm. longa, 0.8–1.0 cm. lata. *Culmi floriferi* c. 30 cm. alti, puberuli, vaginis paulum inflatis, non nunquam puberulis. *Spiculae masculae* 5 in verticillis; pedicelli 2–3 mm. longi, basi barbati, alibi sparse puberuli; glumae 2.0–2.5 mm. longi, bi- vel tri-nerves, nervis connectentibus saepe conspicuis, basi latae, acutae, glabrae vel ciliatae; lemma 3.5–4.5 mm. longum elliptico-lanceolatum, acutum, costa et nervis marginalibus satis prominentibus, nervis connectentibus prominentibus; palea lemma similis, quinquenervis, obtusiuscula; stamina c. 25 in fasciculam unam plus minusve conjuncta; lodiculi breves, lati (fig. 19). *Spiculae feminae* uniseriatae; glumae 6 mm. longae, late ovatae, obtusae, marginibus ciliolatae; lemma paleaque 6 mm. longae, ovatae, acutae, glabrae. *Spicula terminalis* femina. (Plate 9.)

*Distribution*.—BOLIVIA, Dept. of La Paz, San Carlos, Mapiri Region, 850 m. O. Buchtien 458. Dec. 1926. Typus in U.S. Nat. Herb. Duplicate in Herb. N.Y. Bot. Gard.

Mapiri, 5,000 ft., April 1886. H. H. Rusby 232. U.S. Nat. Herb. and Columbia University Herb. Cochabamba, A. Miguel Bang 847 a. U.S. Nat. Herb. and Columbia University Herb. Rurenabaque, San Buenaventura, alt. 1,000 ft. Cardenas 1889. Jan. 1912. U.S. Nat. Herb. Same loc., 'In damp sandy forest', alt. 1,000 ft. O. E. White 880. Aug. 1921. U.S. Nat. Herb. and

Herb. N.Y. Bot. Gard. Rio Chimate, 1900 ft., April 1926, G. H. H. Tate 524. Herb. N.Y. Bot. Gard. PERU, Dept. Junin, Rio Pinedo, north of La Merced, 700-900 m., May 1929, Killip and Smith 23625. 'Dense woods.' U.S. Nat. Herb.

This species has generally a very characteristic appearance owing to the convex indurate pedicels of the male spikelets being of much lighter colour than the glumes and lemmas. It occurs very nearly as far south as *P. monothalma*, and at far greater altitudes (up to 5,000 ft.), and is, therefore, probably the most hardy member of the genus.

16. *PARIANA TRICHOSTICHA* Tutin, sp. nov.

Affine *P. bicolori* sed vaginis tomentosis, costa supra linea conspicua tomenti praedita, pedicellis linea media valde prominente praedita.

*Herba* perennis. *Culmi steriles* 50-60 cm. alti, satis robusti, non nunquam dense brunneo-tomentosi, vaginis dense brunneo-tomentosis, ad orem fimbriatis. *Folia* 13-25 cm. longa, 4.0-6.0 cm. lata, lanceolata, acuta, utrinque glabra; petioli 5-7 mm. longi, 2-3 mm. lati, supra canaliculati, utrinque tomentosi. *Inflorescentia* 6 cm. longa, 7-9 mm. lata. *Culmi floriferi* c. 30 cm. alti, vaginis valde inflatis, tomentosis sed minus quam culmorum steriliu, ad orem sparse fimbriatis. *Spiculae masculae* pedicellis 3.0-4.0 mm. longis, basi pubescentibus, jugo medio longitudinale conspicuo praedita; glumae 1.5 mm. longae (non nunquam longiores sed tunc latissimae), 2-3-nerves glabrae, vel marginibus ciliatae, acutae vel obtusiusculae, plus minusve triangulares; lemma 4.5-5.0 mm. longum, ovato-ellipticum, obtusiusculum, costa et nervis marginalibus satis prominentibus, nervis connectentibus nonnullis satis obsoletis; palea quam lemma paulum brevior distincte quinquenervis, marginibus involuta, satis indurata (fig. 20). *Spiculae feminae* alternatae; glumae 7 mm. longae, lanceolatae, acuminatae, delicatissimae, costa prominente, breviter appressequae sericeo-pubescentes; lemma paleaque 5 mm. longae, apiculatae, glabrae. *Spicula terminalis* sterilis. (Plate 9.)

*Distribution*.—PERU, Dept. Loreto, Mishuyacu, near Iquitos, alt. 100 m., Oct.-Nov. 1929. G. Klug 209. Typus in U.S. Nat. Herb. no. 1455210. Duplicate in Herb. N.Y. Bot. Gard. Iquitos, alt. 120 m., March-April 1930. Llewelyn Williams 8063. U.S. Nat. Herb. and Gray Herb. Yurimaguas, Spruce, s.n., Herb. Kew. COLOMBIA, Intendencia del Choco, Tutunendo, 20 km. north of Quibdo, alt. c. 80 m., May 1931. W. A. Archer 2149 and 2124. U.S. Nat. Herb.

The Colombian specimens are less tomentose, and have somewhat smaller leaves than the Peruvian ones, but further collecting will probably provide intermediates between the two forms.

The distribution of this species is peculiar, as the Peruvian localities are on the eastern side of the Andes, while the Colombian one is considerably to the north and on the western side. Archer 2149 gives the vernacular name as

'Canutillo', and has the note 'leaves used to wrap up Gold and Platinum dust'. This is the only record of any species of *Pariana* being of economic importance.

17. *PARIANA ZINGIBERINA* Doell in Mart. Fl. Bras. ii, pt. 2, p. 337 (1877).

Sterile culms with puberulous sheaths, the upper few only bearing leaves, the remainder leafless; sheaths distinctly auricled at the mouth, fimbriae few, erect. Leaves narrow, oblong-lanceolate, acuminate, 8–10 cm. long, 1.5–2.0 cm. wide. Fertile culms leafless, sheaths somewhat inflated, more or less ribbed. Inflorescence stout; pedicels of male spikelets pubescent at the base, about 3 mm. long; glumes 3 mm. long, 1–2-nerved, one nerve much more prominent than the other, rather broadly triangular, acute; lemma 4.5–5.5 mm. long, oblong, lanceolate, acute, midrib and lateral nerves fairly prominent, sinuous horizontal connecting nerves obscure (fig. 21).



FIGS. 21–23.—Male spikelets,  $\times 2.5$ . 21. *P. zingiberina* Doell, from Altson 314 in Herb. Kew. 22. *P. simulans* Tutin, from type-specimen. 23. *P. concinna* Tutin, from type-specimen.

Glumes of the female spikelets 7 mm. long, puberulent, 1-nerved, keeled, lanceolate, rather narrow; lemma and palea 6 mm. long, ovate acute, curved round the fruit, indurate, lemma scaberulous near the apex, palea smooth. Lodicules 3 small (c. 0.25 mm. long), ragged.

*Distribution*.—BRAZIL, Prov. of Para, in silvis ad Canuma. Martius, Iter Brasil. Type in Herb. Munich.

BRITISH GUIANA, Mazaruni River, Altson 314. Herb. Kew. and U.S. Nat. Herb.

VENEZUELA, between La Guaira and Rio Grande, State of Gaurico, Curran and Haman 1036, June 1917.

The name is spelt 'zinziberina' in 'Index Kewensis', but this is an error.

18. *PARIANA SIMULANS* Tutin, sp. nov.

A *P. zingiberina* Doell, auriculis ad orem vaginae nullis, glumis triangularibus bi- vel tri-nervis, setis praeditis, lemmate minore angustiore differt.

*Herba* perennis, caespitosa. *Culmi* steriles c. 60 cm. alti, tenues; vaginae inferiores, quam internodi multo breviores, glabrae, satis nitentes, laminas

minimas ferentes; vaginae superiores densae, quam internodi longiores, costatae, ad orem fimbriis erectis paucis praedita; ligula brevissima. *Folia* 8–12 cm. longa, 2.0–2.5 cm. lata, oblonga, acuminata, basi satis abrupte contracta, utrinque glabra, supra aliquanto nitentia; petioli brevissimi, supra puberuli, subtus glabra. *Inflorescentia* 3.5–4.5 cm. longa, 8–10 mm. lata, ab vagina summa vix exserta. *Culmi floriferi* c. 30 cm. alti, vaginis valde inflatis, glabris et praeter summam quam internodis brevioribus. *Spiculae masculae* 5 in verticillis omnibus, verticillis densis; pedicelli 3 mm. longi, margine ciliati, dorso puberuli; glumae 2–3 mm. longae, bi- vel tri-nerves, apice seta praedita, triangulares, marginibus versus basin ciliatae; lemma 4 mm. longum, angustum, aliquanto asymmetricum ab basi versus apicem attenuatum, obtusiusculum, costa prominente nervis marginalibus satis obscuris, nervis connectentibus sinuosis, saepe obliquis bijugisque utrinque circiter 2 versus apicem; palea lemma subaequans tenuissima membranacea marginibus involuta; stamina c. 20, filamentis in fasciculis tribus junctis non nunquam paucis libris; lodiculi 0.25 mm. longi, oblongi, ciliolati (fig. 22). *Spiculae feminae* uniseriatae, glumae lanceolatae acuminatae, 6 mm. longae; lemma paleaque ovatae obtusiusculae 5 mm. longae; sparse puberulae; stigmata pilis longis tenuibus praedita. *Spicula terminalis* sterilis. (Pl. 10.)

*Distribution.*—PANAMA, Province of Colon, Loma de la Gloria, in forests; alt. 10–104 m., August 1911. H. Pittier 4075. Typus in U.S. Nat. Herb. COLOMBIA, Intendencia del Choco, La Concepcion, 15 km. east of Quibdo, alt. c. 75 m. W. A. Archer 2213, April–May 1931. U.S. Nat. Herb. A form with slightly broader leaves and larger spikelets than the type.

#### 19. *PARIANA CONCINNA* Tutin, sp. nov.

A *P. zingiberina* Doell et *P. simulante* Tutin foliis longis angustis, glumis subulatis, pedicellis glabris, inflorescentia angusta compacta differt.

*Herba* perennis caespitosa. *Culmi steriles* tenues lignosi ad nodos valde inflati, 30–40 cm. alti; vaginae inferiores aphyllae quam internodii multo breviores, superiores 4–6 quam internodii aliquanto longiores, ad orem fimbriis paucis parvis erectis praedita, folia ferentes; ligula brevissima. *Folia* 12–14 cm. longa, 1.5–2.5 cm. lata, lineari-lanceolata, acuta, utrinque glabra, petiolis 3–4 mm. longis, utrinque puberulis. *Inflorescentia* 5.5 cm. longa, 5–6 mm. lata, vix ex vagina summa exserta, compactissima. *Culmi floriferi* 30 cm. alti, vaginis paulum inflatis, praeter summam quam internodiis brevioribus. *Spiculae masculae* pedicellis 2 mm. longis, glabris; glumae 3.5–4.0 mm. longae, 2- vel 3-nerves subulatae glabrae; costa et nerves satis obscuris, nervis connectentibus utrinque 2 vel 3 in parte superiore; palea quam lemma aliquanto brevior membranacea marginibus involuta; stamina c. 15 filamentis in fasciculam unicam conjunctis; lodiculae glabrae (fig. 23). *Spiculae feminae* uniseriatae, glumae ovatae acutae carina ciliatae, 5.0 mm. longae; lemma paleaque obtusiuscula, 4.0 mm longa. *Spicula terminalis* sterilis.



*Distribution*.—BRAZIL, Prov. of Amazonas, Barra do Rio Negro (Manãos), in forest, Feb. 1851, R. Spruce 1787. Typus in Herb. Kew. The type of this species is under the same number as the type of *P. gracilis* Doell and is the only specimen so far known.

Since it appears to be quite distinct from any other species, it seems best to describe it, rather than to leave it unidentified, as has been done with imperfect specimens which could not be exactly matched with anything.

### GRACILES.

#### 20. *PARIANA GRACILIS* Doell in Mart. Fl. Bras. ii, pt. 2, p. 337 (1877).

Sterile culms fairly stout, sheaths closely imbricate towards the summit, distinctly auricled at the mouth, fimbriae absent. Leaves 2–several, oblong-lanceolate, acuminate, 10–15 cm. long, 2.0–2.5 cm. broad; ligule 2.0–2.5 mm. long. Fertile culms leafless, inflorescence slender, male spikelets scarcely imbricate, their pedicels 2.5–3.0 mm. long, pubescent; glumes 2.0–3.0 mm. long, 1-nerved, acute; lemma 4.0–4.5 mm. long, oblong-acute to ovate mucronate, glabrous, nerves rather obscure, connecting nerves sometimes present (fig. 24). Glumes of the female spikelet 5 mm. long, acute. Terminal spikelet sterile.

*Distribution*.—BRAZIL, Spruce 1787, Manãos, Rio Negro, August 1851, type.

BOLIVIA, d'Orbigny 147, Majes.

PERU, Schunke A 45 above San Ramon, Dept. Junin; 1300–1700 m. in dense forest.

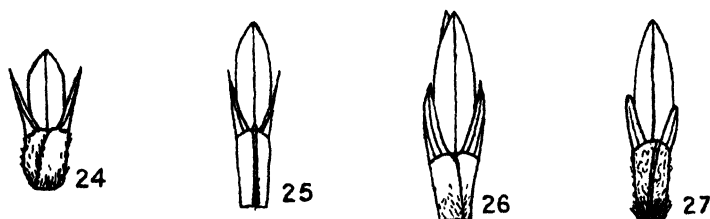
This was until recently the only known species of the Graciles, and is by far the most widely distributed. So far as can be judged from the scanty records at present available, it occurs throughout the valley of the Amazon and its southern tributaries from Manãos to the Andes, where it ascends to 1,700 m. in Peru. The remaining three species of the group appear to be confined to British Guiana, where they all occur in the valley of the Potaro, a tributary of the Essiquibo, which has a peculiar and interesting flora.

#### 21. *PARIANA PULCHERRIMA* Tutin, sp. nov.

A *P. debile* Tutin spiculis 5 non 4 in verticellis omnibus, pedicellis minus pilosis, glumis spiculae feminae glabrae; a *P. gracile* Doell glumis minoribus glabris, glumis spiculae feminae glabrae, et habitu; a *P. Gleasonii* Hitchc. foliis minoribus ex toto levibus, caule brevior, glumis spicularum masularum acuminatis, pedicellis glabris differt.

*Herba* perennis caespitosa stolonifera. *Culmi steriles* 30–40 cm. alti, robusti; vaginae inferiores aphyllae plus minusve imbricatae et inflatae, glabrae, ore valde auriculatae saepe breviter fimbriatae; superiores 2- vel 3-foliatae. *Folia* 10–20 cm. longa, 3–6 cm. lata, glabra levia, subtus glauca, petiolis c. 5 mm. longis. *Culmi floriferi* satis robusti, c. 30 cm. alti; vaginae quam internodi saepissime breviores inflatae glabrae.

*Inflorescentia* c. 7 cm. longa, tenuis, vaginam superiorem saepissime c. 3 cm. superans. *Spiculae masculae* 5 in verticillis omnibus, pedicellis 5 mm. longis, saepe ad costas breviter cano-pubescentibus, paribus fusae, quinta spiculae feminae opposita; glumae 3-4 mm. longae, uninerves, acuminatae; lemma 5 mm. longum, uninerve; palea lemma subaequans; stamina c. 6 paribus fusa (fig. 25). *Spiculae feminae* alternatae; glumae 6 mm. longae, uninerves, abrupte acutae vel apiculatae glabrae; lemma 5 mm., longum, acutum,



FIGS. 24-27.—Male spikelets,  $\times 2.5$ . 24. *P. gracilis* Doell, from cotype in Herb. Kew. 25. *P. pulcherrima* Tutin, from type-specimen. 26. *P. Gleasoni* Hitchc., from Tutin 545 in Herb. Mus. Brit. 27. *P. debilis* Tutin, from type-specimen.

glabrum; palea 5 mm. longum, obtusum, glabrum; lodiculi 3 mm. longi oblongi truncata ovarium aequantes et ante anthesin id involventes. *Fructus* non visus. (Pl. 10.)

*Distribution*.—BRITISH GUIANA, Potaro River, Tutin 466; near the landing at Kangaruma in a damp shady place on clay soil by the river, 19 August 1933. Typus in Herb. Mus. Brit. Jenman 856, Kaietuk ('Kaieteur') savanna, Potaro River. Herb. Kew. and Herb. Mus. Brit.

The pedicels of the male spikelets are yellowish, while the lemmæ are generally red or purple, giving a striking banded appearance to the inflorescence, even when the flowers are not open. The under side of the leaves is also often purple with a glaucous bloom and the sheaths are frequently similarly coloured.

22. *PARIANA GLEASONI* Hitchcock in Contrib. U.S. Nat. Herb. xxii, pt. 6, p. 513.

Sterile culms about 2 mm. in diameter, somewhat swollen at the nodes, lower sheaths much shorter than the internodes, upper one or two equalling or exceeding the internodes and alone bearing leaves, all ribbed and puberulous between the ribs, fimbriae sometimes present but not exceeding 1 mm. long. Leaves one, rarely two, up to 30 cm. long and 8 cm. wide, lanceolate-acuminate, narrowed into a petiole about 3 mm. long and 2 mm. wide, pubescent and somewhat channelled above, glabrous and convex below; ligule about 1 mm. long. Fertile culms about 20 cm. high, slender, uppermost sheath inflated, ribbed, glabrous, often bearing a short, erect, almost setaceous lamina. Inflorescence

slender, whorls of spikelets distant, pedicels of male spikelets 4 mm. long, shortly pilose below, glabrescent above; glumes 2.5–3.0 mm. long, rather unequal, 1–2-nerved, acute to acuminate; lemma 4.5–5.5 mm. long, oblong, midrib and marginal nerves more or less prominent, obscure connecting nerves sometimes present (fig. 26). Female spikelets in one row; glumes 6 mm. long, 1-nerved, oblong-lanceolate, sparsely pubescent, ciliate on the margins, acute, the lower keeled and the upper rounded on the back; lemma and palea 5 mm. long, ovate, apiculate, glabrous, both very much wrapped round the fruit, the lemma 1-nerved, the palea 2-nerved; lodicules three, 1 mm. long, oblong, truncate; style very short and thickened, stigmas two; ovary 2 mm. long, glabrous. Terminal spikelet sterile, glumes about 4 mm. long, incurved, lemma shorter, palea sometimes missing.

*Distribution*.—BRITISH GUIANA, Potaro River, Gleason 209, Potaro Landing, in dense upland bush, June 25–27, 1921. Type in U.S. Nat. Herb. no. 1064516. Gleason 249, Potaro Landing, 312, 438, Tumatumari, Potaro River, in U.S. Nat. Herb. and Herb. N.Y. Bot. Gard. Jenman 7526 in Herb. Kew. Tutin 545, in mixed forest, Tiger Creek, Tumatumari, in Herb. Mus. Brit. Growing in large tufts in fairly open places. Glumes green with purple veins, palea translucent, purple-brown.

Hitchcock's statement that the terminal spikelet is fertile appears to be an error, as the terminal spikelet is missing in the type.

### 23. *PARIANA DEBILIS* Tutin, sp. nov.

Ab aliis speciebus seriei spiculis maculis 4 (vel raro 5) in verticellis omnibus, glumis spiculae feminae sine nervis discedit.

*Herba* perennis caespitosa. *Culmi steriles* tenues, 28–32 cm. alti; vaginae inferiores aphyllae glabrae, ore obliquae, auriculis parvis nullisve, fimbriis nullis; vaginae superiores 2 vel 3, foliatae. *Folia* lanceolata acuminata, glabra, 10–15 cm. longa, 2.5–3.5 cm. lata, petiolis 3–5 mm. longis, tanquam vaginis non nunquam minute puberulis. *Culmi floriferi* tenues, 15–20 cm. alti, vaginis quam internodiis brevioribus, inflatis, inter costas minute puberulis. *Inflorescentia* c. 3 cm. longa, tenuis rhacide facile disarticulanda, vagina superiore 3–5 cm. sub basin inflorescentiae terminante. *Spiculae masculae* 4 vel raro 5, in verticellis omnibus, satis patentes, pedicellis 4–5 mm. longis, pilis appressis sericeis albis vestitis, paribus fuis; glumae 1.0–2.5 mm. longae, uninerves, obtusae, glabrae; lemma 5 mm. longum, anguste ellipticum obtusiusculum valde uninerve glabrum; palea quam lemma paulum brevior glabra; stamina circa 8 (fig. 27). *Spiculae feminae* alternatae; glumae 5.5 mm. longae, sine nervis, lanceolatae acuminatae puberulae; lemma 5.0 mm. longum ovatum apiculatum glabrum; palea 4.5 mm. longa, ovata apiculata glabra; lodiculi 0.5 mm. longi truncati ovati. *Spicula terminalis* sterilis; glumae subulatae, lemma superantes. *Fructus* 4 mm., longus 2 mm., diametro obtuse trigonus glabrus, basi styli persistente,

*Distribution*.—BRITISH GUIANA, Potaro River, Tutin 573 ; in the Gorge about a mile below Kaietuk Fall, shady stony ground sloping steeply to the river, 22 August 1933. Typus in Herb. Mus. Brit.

EXCLUDED SPECIES.—*Pariana angustifolia* Spreng. Syst. ii, p. 609 (*Panicum triticeum* Willd.) is a species of *Chusquea* (R. Pilger, in litt.).

#### EXPLANATION OF THE PLATES.

##### PLATE 8.

*Pariana imberbis* Nees. (Burchell 9265 in Herb. Kew.)

*Pariana lanceolata* Trin. (Riedel, specimen in Herb. Kew.)

##### PLATE 9.

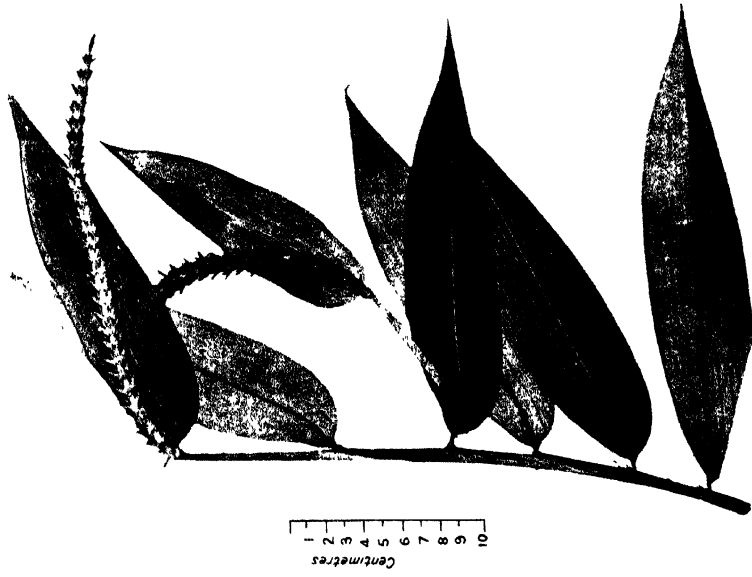
*Pariana bicolor* Tutin, sp. nov. (Type-specimen. Buchtien 458 in U.S. Nat. Herb.)

*Pariana trichosticha* Tutin, sp. nov. (Type-specimen. Klug 209 in U.S. Nat. Herb.)

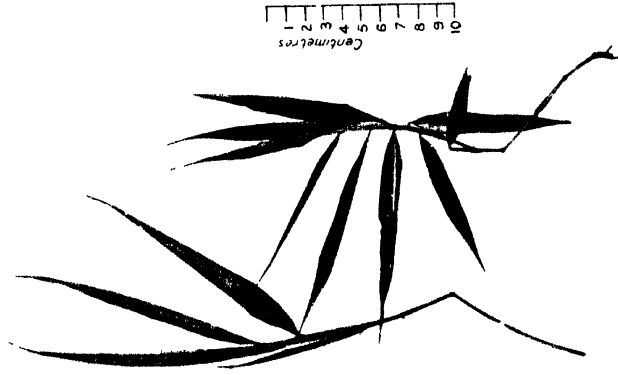
##### PLATE 10.

*Pariana simulans* Tutin, sp. nov. (Type-specimen. Pittier 4075 in U.S. Nat. Herb.)

*Pariana pulcherrima* Tutin, sp. nov. (Tutin 466.)



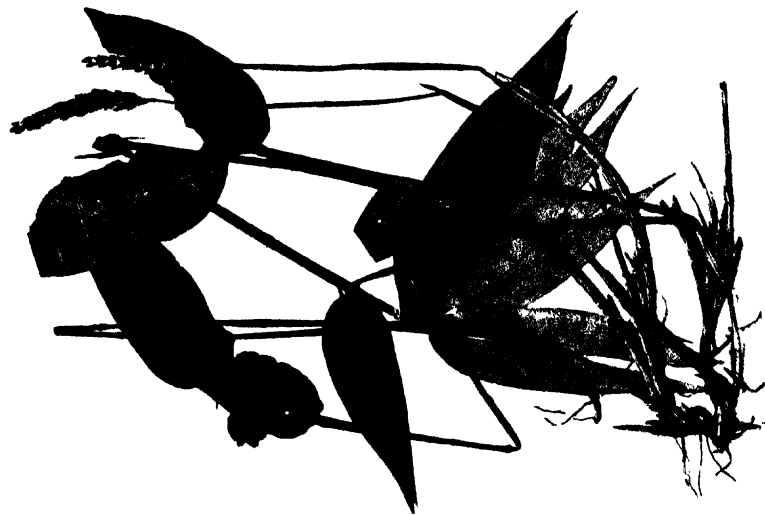
PARIANA IMBERBIS NEES



PARIANA LANCEOLATA TRIN.



TUTIN



PARIANA BICOLOR, SP. NOV.

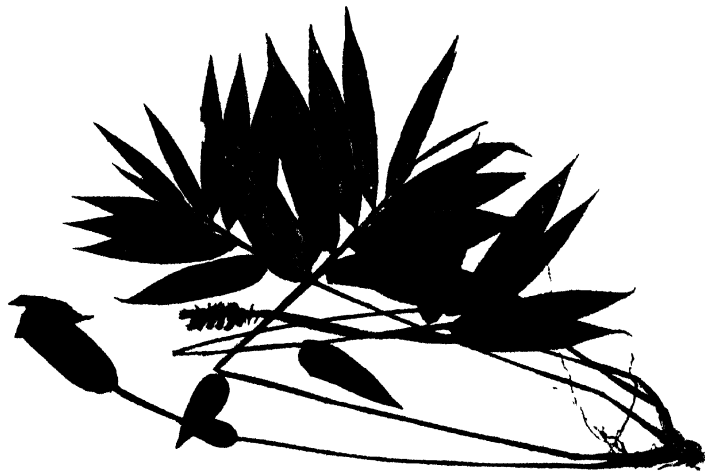


PARIANA TRICHOSTICHA, SP. NOV.

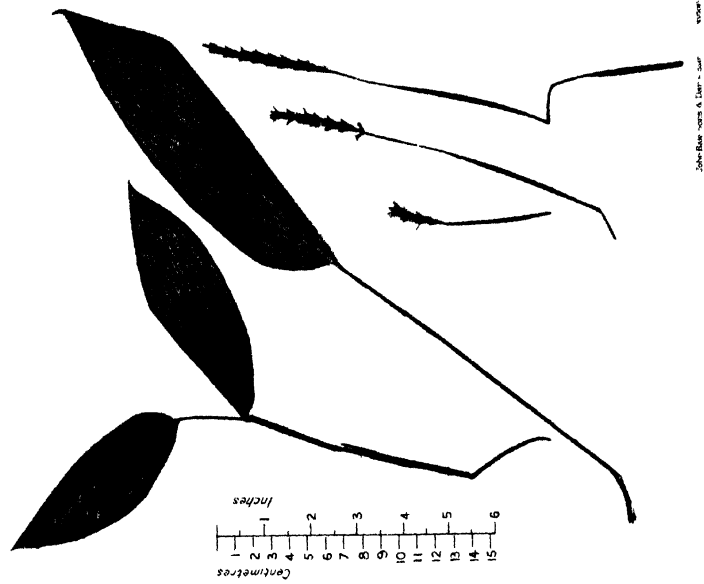
— 1874 —







**PARIANA SIMULANS, SP NOV.**



**PARIANA PULCHERRIMA. SP. NOV.**



The floral morphology and cytology of *Elettaria Cardamomum* Maton\*. By  
P. J. GREGORY, M.A., F.R.M.S., F.L.S. (From the Cytological Laboratory,  
Department of Botany, University of London, King's College.)

(PLATES 11-13 and 10 Text-figures)

[Read 24 January 1935]

#### INTRODUCTION.

*Elettaria Cardamomum* (commonly known as Malabar Cardamon) is a perennial plant belonging to the family Zingiberaceae. It has a uniquely restricted distribution, being confined to some parts of South India and Ceylon, and is cultivated extensively in Malabar and Ceylon for its aromatic seed, which is one of the renowned spices of the East. The word 'Elettaria' can be split up into two Malayalam words, 'Ela' meaning leaf and 'Tari' or 'Ari' meaning seed, the name as a whole implying a leafy plant with seed-like fruits. The general habit of the plant, with seed-like fruits borne on a long spike originating from a rhizome, suggests the possible derivation of the name as well as its original home.

Years of cultivation have not widened the range of its distribution, even to extensive regions in India, probably due to its specific environmental requirements. It grows only at altitudes of about 2,000-3,000 feet above sea-level, in areas having a regular alternation of wet and dry weather, the high ranges of Western Ghats providing the most suitable climatic conditions. Cultivation is on a large scale in this area, affording a chief source of income to the State as well as to the ryots. The plant has a growth period of about four years, and the flowering begins with the first fall of rains in April or May of the fourth season. The fruits take about six months to ripen, and they are generally collected in October and November.

Owing to its economic importance and in view of the fact that its cytology—even the chromosome number—had not been worked out, the plant was suggested by Prof. Gates as suitable for detailed investigation. In addition to the cytology, a detailed examination of the floral morphology was made in the paper.

#### MATERIAL AND METHODS.

Flowers of *Elettaria* were collected in May 1932 from a Cardamon estate at Peermede in Travancore. Flower-buds in various stages of development were fixed in the following fluids, an air-pump being used to ensure thorough penetration of the fluid.

\* Thesis approved for the degree of Doctor of Philosophy in the University of London.  
LINN. JOURN.—BOTANY, VOL. L

The fixing fluids were :—

- (1) Flemming's medium fluid.
- (2) Flemming's strong fluid.
- (3) La Cour's fluids 2B and 2BE.
- (4) Bouin's fluid.
- (5) Allen's modification of Bouin's fluid.

Of these, Flemming's medium fluid and La Cour's 2BE gave the most satisfactory results. While for cytological investigation younger buds were specially selected, a more extensive collection comprising flowers in all stages of development was made and preserved in 4 per cent. formalin. Root-tip materials were collected at the Royal Botanic Gardens, Kew, with the permission of the Director, and fixed in fluids (1), (2), and (3). As the work progressed, further supplies of flower materials were obtained through the courtesy of the Department of Botany of the College of Science, Trivandrum, S. India.

Cytological materials were fixed according to the scheme given by La Cour (1931). Paraffin sections were cut of thickness 6–20  $\mu$ , and stained in Iodine-Gentian violet. For morphological studies, the thickness of the sections ranged from 10–30  $\mu$ , and they were stained also in some cases with Safranin.

#### SECTION A.—FLORAL MORPHOLOGY.

##### *Description of the inflorescence and flower.*

The flowers are borne on spicate racemes which originate horizontally from the tuberous ringed part of the rhizome. On this common spike, which is about 18–28 inches long, flower groups of three or occasionally four are borne alternately, each in the axil of a bract, each flower being again subtended by a bracteole. Usually in a flower group one flower will be fully developed and the others will be in the bud-stage, as shown in fig. 1.

The floral parts of the flower are shown in fig. 2. They are arranged on the trimerous ground-plan of the Monocotyledons, but the members of the successive whorls originate in a close spiral series. The calyx forming the outermost whorl is tubular, having three tooth-like lobes at the apex. The corolla or the second whorl of perianth is tubular below and divided into three distinct lobes above. Each petal lobe is oblong-linear with slightly inflected margins and ends turned up at the edges slipper-wise. The members of this whorl alternate with those of the calyx whorl. On the throat of the corolla tube are the members of the two staminal whorls. The pistil is composed of a trilocular inferior ovary with a filiform style ending in a capitate stigma. By the side of the style in the antero-lateral position are two epigynous glands (*x* & *y*) (fig. 3 ZZ).

As the work progressed, it became evident that two or three problems in floral morphology required re-investigation. To begin with, there is the question of the exact morphological nature of the labellum and its relation to other

members of the staminal whorls. 'The morphology of the flower has been the subject of much discussion as regards the part played by the androecium' (Rendle, 1930). Associated with this is the determination of the morphological value of the structures ( $x$  &  $y$ ). Finally, there is the question of the gynoeceium and its morphological nature.

In the past, the problems of floral morphology have been studied in three different ways. The palaeontological method is of recent origin, and, though limited in its scope and application, has been ably advocated by Hamshaw

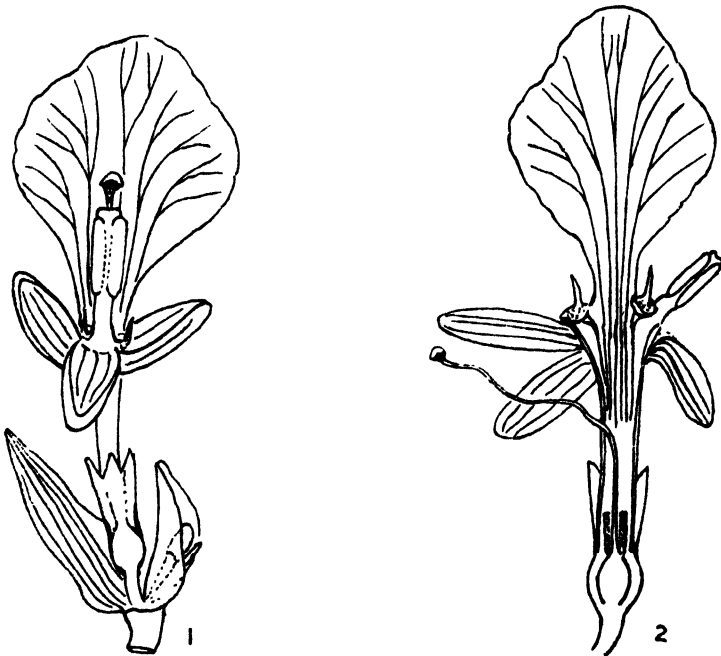


FIG. 1.—Group of three flowers, one highly developed, while the other two are in the bud-stage. Nat. size.

FIG. 2.—Diagram to illustrate the parts of the individual flower. Note the position of the two epigynous glands at the base of the style. Nat. size.

Thomas in his studies of Pteridospermous plants (1933). The ontogenetic or developmental method is a useful one, and Payer (1857) was its most ardent exponent. Lastly, there is the method of vascular anatomy. The place of vascular anatomy in morphological enquiry was raised to distinction by the researches of Van Tieghem (1868), who saw in the arrangement, number, and disposition of the vascular strands a clue to the puzzling variations in the external form of floral organs. The evidence and conclusions in this investigation are mainly based on the last method.

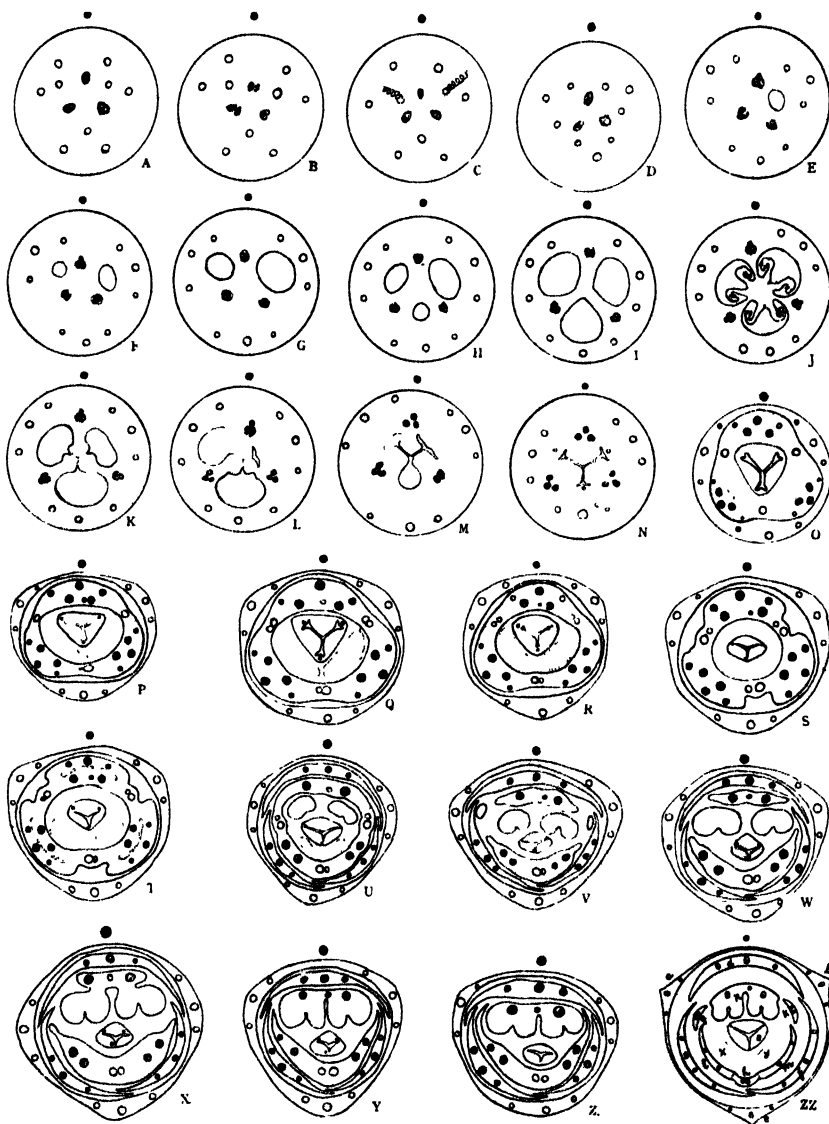


FIG. 3.

- A, showing 12 vascular strands at the pedicel region, 9 peripheral ones (unshaded) and three central ones (shaded).  
 B, region showing the apparently dual nature of each bundle of the central group.  
 C, the shifting to the exterior of the two median bundles of the peripheral groups.  
 D, showing the altered disposition of the bundles after the three median ones of the peripheral groups have shifted to the exterior.  
 E-I, the spirality in the levels of origin of the ovarian cavities is represented,  
 J, ovular region showing the two series of ovules in each loculus,

EXPLANATION OF FIG. 3 (*cont.*).

- K-M, showing the termination of the ovarian cavities in the same spiral sequence.  
 N, showing the region where each central bundle divides into three branches, one external and two internal.  
 O-U, stages showing the further course of the branches of each central bundle. It is seen that the outer of the three remains as the central bundle of the petal, while the two internals proceed into a member of the inner staminal whorl.  
 P-T, stages showing the separation of the staminal whorls from the corolla whorl.  
 U, showing the bundle disposition of all the whorls. Note the six groups of bundles in the two staminal whorls in one ring, of which the alternate groups are unshaded to show their origin from the peripheral groups.  
 V, region at which the terminal points of the two postero-lateral staminodes of the outer whorl are seen.  
 W-Z, successively higher regions at which the floral parts differentiate fully.  
 ZZ, diagrammatic cross-section of the flower including the staminodes and the epigynous glands ( $x$  &  $y$ ), showing the number and disposition of the vascular strands in each organ. Note the absence of vascular strands in the glands. For explanation of the parts, *vide* text, p. 369.

The twenty-seven figures marked A-ZZ are drawn from transverse serial microtome sections— $20\mu$  in thickness—from the pedicel to the apex of a flower-bud to illustrate the course, number, and disposition of the vascular bundles as well as the origin and termination of the ovarian cavities in spiral sequence. It is worthy of special note that, since the difference in level in the origin of successive ovarian cavities is about  $60\mu$ , the fact of spirality in their origin and termination could not be observed in hand-sections.  $\times 60$ .

*The labellum.*

There is no controversy about the morphological nature of the perianth whorls. The structures that are mostly disputed are the two staminal whorls and the constitution of the labellum. In the literature the members of the staminal whorls are given various positions and the labellum has been interpreted in different ways. In examining sections of flower-buds at various stages of development it became evident that the number, disposition, and composition of the vascular strands had a certain definiteness and regularity in relation to floral members, and so the study was pursued in several sets of serial microtome sections from pedicel to the apex of the flowers. The disposition, number, &c., are shown somewhat diagrammatically in fig. 3, and the twenty-seven figures are numbered from A-ZZ. The letters in the following description refer to this figure, the dot above each figure indicating the posterior position.

At the pedicel region (fig. 3 A) there are twelve vascular strands in groups of three; three bundles forming the central group are shaded to differentiate them from the nine unshaded peripheral bundles. This scheme of shading is continued in subsequent figures to distinguish the branches of the central group from those of the three peripheral groups. The median bundles of the peripheral groups occupy a position inner to the laterals of the same group. In B, the apparently dual nature of each bundle of the central group is seen, which is not so clear at the higher level shown in C. Again, in C the median

bundle of each peripheral group, which is inner to the lateral ones in fig. A, is seen to shift its position to the exterior, and its altered position in relation to the lateral ones of the same group is seen in D. This shifting of the positions of the median bundle of the peripheral groups, which is a turning outwards rather than branching of the bundle, is significant, as will be shown later. In E-I the origin of the ovarial cavities in spiral sequence is represented. The central group presents a diffused nature and occupies the placental region of the ovary. At the ovular region represented in J the central group supplies branches to the ovules. K-M show the successive stages at which the ovarial cavities terminate, indicating the same spiral sequence. This fact of origin and termination of the ovarial cavities in the same spiral sequence is very significant in the consideration of the morphological nature of the gynoeceum. The central group of bundles below the ovarial cavities have now separated to form what we may designate the placental bundle. In N each placental bundle is dividing into three, one external and two internal. In the subsequent stages (O-U) it is seen that the outer one continues as the central bundle of the petal, while the internals continue as two bundles of each member of the inner staminal whorl. In fig. O the triradiate cavity of the style is seen to be exactly above the ovarial cavities, as shown by reference to the sepal bundles, and shows the three stylar bundles on the dorsal suture, thus presenting no anomaly in the disposition of the ovarial and stylar cavities. Again, on the angular sides of the style opposite the sepals are seen three bundles (unshaded), which take their origin from the branches of the peripheral group (fig. 3 N), and can in later figures be traced to bundles in the two postero-lateral staminodes, while the posterior one passes on to the bundle group in the middle part of the labellum. This fact is significant as regards the morphological nature of that organ.

Stages P-T show the separation of the staminal whorls from the corolla whorl, and, finally, in U the corolla is completely separated from the former, showing the bundle disposition of the two whorls or organs. The corolla whorl shows three distinct petals, each having three bundles. The two staminals, which are actually in a single ring, show six groups of bundles, alternate groups occupying positions opposite the sepals and petals respectively. Of the three groups opposite the sepals, the postero-laterals can be traced to the staminodes in same position seen in V, while the anterior one passes into the central region of the labellum. Of the three groups of bundles opposite the petals the posterior one passes into the filament of the fertile stamen, while the antero-laterals persist in the lateral region of the labellum (V). It is important to note here that the bundle groups opposite the sepals are a continuation of the peripheral groups on the same radii, while those opposite the petals originate from the central groups. Figs. 3 W-Z show successive regions at which the well-differentiated floral parts (calyx whorl, corolla whorl, fertile stamen, labellum, and the style) are seen at successive higher levels in the flower-bud. Here the glands ( $x$  &  $y$ ) and the staminodes are not seen, because the sections are from



levels above the terminal points of those structures. So, to facilitate easy description during discussion, a diagrammatic cross-section of the flower, including the staminodes and the glands with the vascular disposition of each member, is shown in fig. 3 ZZ, and the parts are named as follows :—

<i>a, b, &amp; c</i> . . . . .	three sepals of the calyx whorl.
<i>d, e, &amp; f</i> . . . . .	three petals of the corolla whorl.
<i>g, h, &amp; k</i> . . . . .	members of the outer staminal whorl.
<i>l, m, &amp; n</i> . . . . .	parts of the inner staminal whorl.
<i>o</i> . . . . .	the style.
<i>x &amp; y</i> . . . . .	the two epigynous glands.

From the foregoing description of the course of the vascular strands, it is clear that there is a regularity and definiteness in their supply to the floral members. Thus, while the peripheral groups supply bundles to the members of whorls on the same radius (sepals, outer staminal whorl, and style), the central group supplies bundles to whorls on the alternate radii (petals, inner staminal whorl, and ovules). A diagrammatic representation of the course of the bundles in a longitudinal view is shown in fig. 4. One peripheral group of three bundles, shown on the left, starts from the pedicel with the median one internal to the laterals. Soon, below the region of the ovary, the median bundle turns outwards to a position exterior to the laterals, from which its course is continued along the walls of the ovary. These three bundles of the peripheral group, after supplying bundles to the sepals on the same radius, proceed upwards; the laterals then terminate in a member of the outer staminal whorl, while the median one is continued into the same radial position of the style. The course is the same for the other two groups of peripheral bundles. Regarding the course of the central group, one bundle shown on the right side (fig. 4) presents a dual diffused constitution below the ovarial region. It is continued as the diffused placental bundle at the junction of the two ovarial cavities, where it gives branches to the ovules. Later it divides into three branches, the outer one passing into the petal on the same radius and the inner two terminating in a member of the inner staminal whorl. The course is the same for the other two central bundles on the corresponding radial positions.

With these facts we shall try to correlate the position and constitution of the labellum. According to the generally accepted floral diagram of the family, the trimerous floral parts are arranged alternately, the labellum being formed of the two antero-laterals of the inner staminal whorl, the posterior one of the same whorl forming the single fertile stamen. This view assumes the suppression of the anterior member of the outer staminal whorl, while the postero-laterals of the same whorl persist as staminodes.

In tracing the development of the vascular strands with reference to course, number, and disposition, there seems to be sufficient evidence to justify the following modification. At the region where the bundles of all the members are seen (fig. 3, U) there are three groups of vascular strands for each whorl,

as shown in the diagrammatic figure 3 ZZ. The outermost whorl consisting of three sepals (*a, b, c*) has nine bundles. The petals (*d, e, f*), alternating with the sepals, show another series of nine bundles in three groups. Alternating with these and opposite the first whorl are three groups of bundles for members *g, h, k*. As already shown, these bundle groups take their origin from the peripheral group. Of these three groups, the anterior one (*h*) occupies the middle region of the labellum, while the two postero-laterals (*g, k*) can be traced to the staminodes in the same position. Alternating with these are the

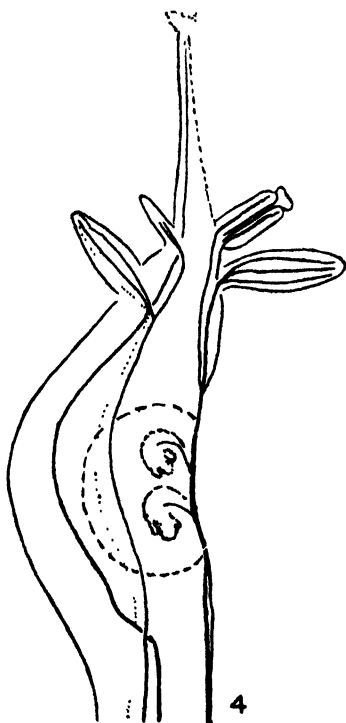


FIG. 4.—Diagrammatic representation of the course of the vascular bundles in longitudinal view. See text.

bundle-groups (*l, m, n*), of which *l* and *m* occupy the lateral region of the labellum, while the posterior group (*n*) passes into the filament of the fertile stamen. Now the presence of these six groups of vascular strands in two alternating series indicates that no suppression of any member of the staminal whorls has taken place. The bundles of the two tooth-like staminodes (in origin, disposition, and structure) correspond to bundle-group *h* in the middle region of the labellum. The fact that they occupy the position opposite the sepals (first whorl) indicates that they belong to the third whorl (the outer staminal whorl). Again, the bundle groups *l* and *m* correspond in position &c. to that (*n*)

in the fertile stamen; these three groups, being opposite the petals (second whorl), should belong to the inner staminal whorl, according to the plan of alternating series of successive floral parts. The fact that one bundle-group (*h*) is similar in origin, disposition, and number to groups *g* and *k* suggests that the morphological entity, labellum, is in fact a composite structure, having in its composition the two antero-laterals (*l* & *m*) of the inner staminal whorl and the anterior member (*h*) of the outer staminal whorl. So the lateral regions of the labellum should belong to the inner staminal whorl, and the facts of observation support this requirement. Further, when the venation of the labellum is examined under the dissecting lens, it is found that the central group of bundles passes down from apex to base, without giving off any lateral branches or showing any connexion with the two groups on either side (fig. 5).

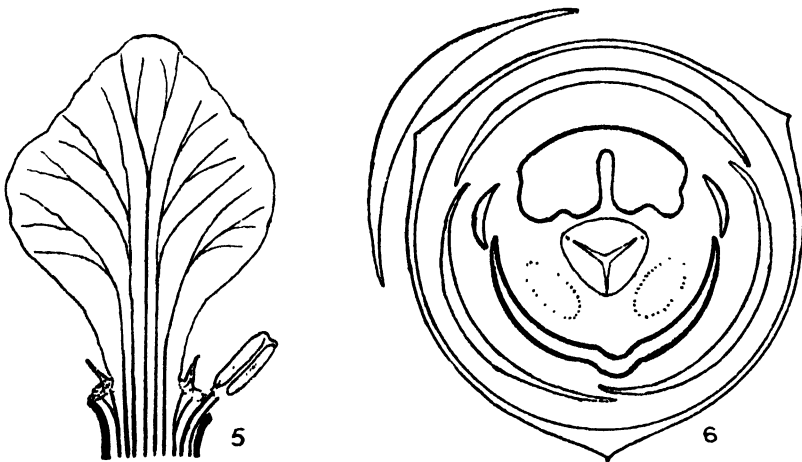


FIG. 5.—Showing the venation of the labellum and the other parts of the two staminal whorls—two pointed staminodes and fertile stamen.

FIG. 6.—The amended floral diagram.

This structural isolation of the central group of bundles in the labellum from the lateral ones lends support to the view here outlined. Finally, even from the external form, with its slightly three-lobed margin (fig. 5), one cannot fail to come to the same conclusion regarding the morphological composition and disposition of the labellum in floral organization. The amended floral diagram is shown in fig. 6.

In addition to these structures, a transverse section shows two glandular bodies (*x* & *y*, fig. 3 ZZ) in the antero-lateral positions between the labellum and the basal portion of the style. These bodies have been examined both anatomically and developmentally; there is every evidence that they are merely glands having some special physiological function. Anatomically

they show closely-packed thin-walled cells with very little tissue differentiation, rich protoplasmic contents with conspicuous nuclei, and, most important of all, the absence of any well-defined vascular supply. Developmentally, also, the fact that they originate below the region where the floral organs are differentiated points to the conclusion that they are new structures arising merely as epidermal appendages of the ovary and not resulting from the transformation of any essential floral organs, as interpreted by previous investigators.

At this stage a critical examination of the various views regarding the morphology of the labellum and the glands seems to be desirable, to show how they appear to be untenable in the light of the present investigation. The first view regards the labellum (in two parts) as a member of the outer staminal whorl only, with the two staminodes (*g* & *k*) completing the whorl. The two glands (*x* & *y*) with the fertile stamen are regarded as the three members of the inner whorl. In the first place, the fact of assuming four members in one whorl is not in harmony with the trimerous ground-plan of the Monocotyledons. Secondly, the plan of alternating position of successive floral parts requires the members of the third whorl (outer staminal) to be opposite to those of the first whorl (sepals), and not opposite the petals, as the two lobes of the labellum would be according to this view. The labellum cannot be considered as being composed of two members of the outer whorl; the only way by which this difficulty could be overcome is to regard the labellum as a unitary structure, and to give it the anterior position in the outer whorl as originally suggested by Robert Brown. But the external form, venation, and vascular anatomy already shown do not support in the least the unitary constitution of the labellum. Another serious objection to this view is that it regards the structures (*x* & *y*) with the fertile stamen as forming the three members of the inner whorl. This presumes the structures (*x* & *y*) to be staminodes or transformed stamens. Developmentally Payer (1857) in *Alpinia nutans* and Baillon (1876) in *Zingiber officinale* have shown that these structures are the last to appear in the respective flowers and that they could be regarded only as glands having no morphological value. -

The second view, which is more or less accepted at the present time, regards the labellum as a part of the inner staminal whorl only, being composed of the two antero-laterals of the inner whorl, the fertile stamen forming the third member. Further, it assumes the suppression of the anterior member of the outer whorl. The supporters of this view are Lestiboudois (1841), Payer (1857), Van Tieghem (1875), Baillon (1876), and Schumann (1904). Finally, Rendle (1930) has adopted it in his general account of Zingiberaceae. This view is a distinct advance on the former one. In the first place, it regards the structures (*x* & *y*) as only glands. Secondly, the respective positions of the members of each whorl agree with the plan of alternating series. But the serious objection to this view is that it merely assumes the suppression of a member. It is not surprising that the earlier workers failed to recognise the flaw in this, because the history and course of the vascular strands could

hardly reveal itself in hand-sections. The view set forth here brings anatomical evidence as well for the glandular nature of  $x$  and  $y$ . Moreover, it explains the constitution of the labellum and its relation to the staminal whorls without any assumption of suppression whatsoever.

Thus, all the six members are accounted for in their respective positions, and the two glandular structures ( $x$  &  $y$ ) are also accounted for. In this connexion, it is necessary to refer to the status given to these organs by McLean Thompson (1933) in his studies on Scitamineae. He regards them as a part of the gynoeceium and calls them stylodes.

### *The gynoeceium.*

The gynoeceium in Angiosperms has been a subject of much discussion and controversy. The views on the subject can be broadly classified into two groups :—

- (a) Carpellary theories.
- (b) Acarpellary theory.

The carpellary theories are mainly two :—

- (1) The monomorphic view.
- (2) The polymorphic view.

*The monomorphic view.*—This, the classical view of carpel constitution, was propounded by Goethe in 1790, and was restated by Goebel in his 'Organography' (1905). According to this view, a monocarpellary gynoeceium is a modified carpellary leaf (megasporophyll) with the margins fusing to form the placenta, the apex of the folded leaf forming the stigmatic surface; a tricarpellary gynoeceium like that of Zingiberaceae is formed of three megasporophylls with the six rows of ovules borne on the axis formed by the fusion of adjacent leaf-margins.

*The polymorphic view.*—This is a modification of the previous one advocated chiefly by Miss Saunders (1923) in *Matthiola* as an explanation of the anomalous position of the Cruciferous replum and the commissural stigma, and extended to other families in subsequent papers (1925, 1927, 1929, 1931). According to this view, the three main functions of the gynoeceium, viz. protection, reproduction, and reception, need not necessarily be performed by the same carpellary leaf as understood by the monomorphic view, but may be distributed to different carpels, thus justifying the appellation of the view. The Cruciferous gynoeceium, according to this view, is composed of four carpels of two types: one, called solid fertile carpel, taking the functions of reproduction (by producing the ovules) and reception (by being stigmatic), while the other, called sterile valve carpel, has only the function of producing a valve or protective cavity for the ovules.

*Acarpellary view.*—This view of the constitution of the gynoeceium was put forward recently by McLean Thompson with regard to the Scitamineae ovary (1933). In the words of the author, 'the ovary in this affinity will be separated

from the style and the stigma and will be considered a receptacular crater, the configuration of which is determined by factors operative in and on the receptacle itself. The style in this affinity will be considered of androecial origin, unstable in construction, and reflective of perversion of essential organs rather than an obligate organ in reproduction and with stigmatism a phenomenon of its present state'. The style and stigma have no morphological connexion with the ovary, which is a mere receptacular crater whose configuration is mainly determined by physiological factors. Moreover, this view regards the two glandular structures ( $x$  &  $y$ ) as stylodes.

With these various views in mind, let us examine the evidence obtained in the present investigation regarding the morphological nature of the gynoeceium. In examining serial microtome sections of various flowers in different stages of development, the important fact was noted that the ovarial cavities do not appear simultaneously at the same level but in spiral sequence (fig. 3 E-I). As expected, the same spiral sequence and orderliness in the termination of these cavities were observed (fig. 3 K-M). This spiral sequence is like that of foliage leaves and various other floral members. In a median longitudinal section the two ovarial cavities in view (fig. 7) are seen at different levels, one originating and ending earlier than the other. Again, this figure indicates that these cavities with the central axis formed by the fusion of the margins of the megasporophylls are continued directly into the style. A cross-section of the stylar region also shows its tri-radiate cavity, with the vascular strands situated at the dorsal suture region of each carpellary leaf. Moreover, in position also they correspond to the dorsal midrib bundle of the ovarial cavities, which is the normal position one would expect from the plan of alternating series of successive floral whorls. The carpellary leaf, being the fifth whorl from the sepals, should occupy a position opposite the latter, and the facts support this. Regarding the placental bundles, their apparent dual and diffuse nature in some regions may well be claimed as an indication of their compound structure—as the monomorphic view postulates,—being formed by the fusion of the marginal bundles of adjacent carpellary leaf-margins. In *Sisymbrium Allaria*, Arber (1931) has shown the same feature, and argues from it the bicarpellary constitution of the cruciferous gynoeceium.

The first problem is to decide whether the gynoeceium is carpellary or acarpellary in constitution. According to the acarpellary view of McLean Thompson, the ovary is separated from the style and the stigma and regarded only as a receptacular crater whose configuration depends mainly on physiological factors. But the direct continuation of the ovarial cavity and the central tissue bearing the ovules into the style as shown in fig. 7 does not support this view, and the separation of the style and the stigma from the ovary is untenable. Even granting the high physiological value which McLean Thompson attributes to the organisation of floral members, it is inexplicable why he should separate these organs which are performing allied functions in connexion with reproduction. Again, the acarpellary view regards the structures ( $x$  &  $y$ ) as a part of the gynoeceium, and calls them stylodes. But the anatomical

evidence set forth above regarding their true nature does not support this assumption. Another serious objection to regarding these structures as organs of any morphological value is their absence in the tribe Costoideae of the family Zingiberaceae. If they are actually transformations of any essential organs, such as stamens or style, there is no reason why they should not be present in all the members of the family. Besides this positive evidence against the acarpellary view, the following direct evidence for the carpellary view may be added. In the first place, there is the spiral sequence in the origin

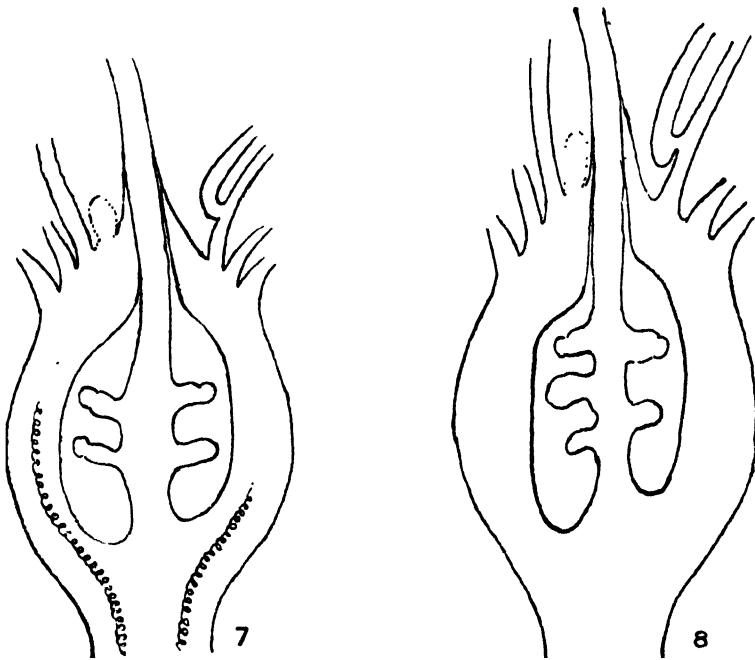


FIG. 7.—Representing the turning to the exterior of the median bundle of the peripheral group and its continuation as the bundle of the ovary wall.

FIG. 8.—Showing the direct continuation of the central tissue bearing the ovules as the style, and the difference in the levels of the ovarian cavities.

and termination of the ovarian cavities (a fact which would reveal itself only in serial microtome sections). Secondly, there is the co-ordination in the disposition of the ovarian and tri-radiate cavities of the style in relation to the sepals. On the monomorphic view, the three carpellary leaves constituting the ovary and the style should be the fifth whorl from the sepals. Evidence from anatomy satisfies all these conditions, in addition to the fact that the three bundles of the style occupy the required positions on the dorsal suture in relation to the ovarian cavity as demanded by the carpellary view.

Assuming the carpellary nature of the gynoeceium we may examine the applicability of the polymorphic view to the gynoeceium of this family. Recent investigations of the Cruciferous flower (Arber, 1931) and criticisms of the conception of carpel polymorphism (Parkin, 1926) have brought forth evidence to question the validity of this view even on the material on which it was founded. Regarding the anomalous position of the commissural stigma in Cruciferae, Arber states, 'That in certain stigmas the carpel margins should play a predominant rôle need not surprise us, when we remember that the main function of the carpel, as originally defined by De Candolle, is the development of ovules on the *margin* of the leaf'. The double contour line on the ovary wall and the different sizes of the loculi of the fruits are taken as strong arguments by Saunders (1925) in support of the polymorphic view. In the cross-section of the ovary shown in Pl. 11, *p*, such a double contour line is absent. Again, in a number of fruits examined, no irregularity in the formation of the loculi was noted. Thus the Zingiberaceous gynoeceium does not present any evidence in support of the polymorphic view. On the other hand, the anatomical evidence is strongly in favour of the monomorphic view. This view, as held at present, cannot, however, be accepted *in toto*; but has to be modified to account for the conditions obtaining in the ovary.

By the very fact that the inferior ovary is sunk in the receptacle, it can only be naturally described as a crater (McLean Thompson, 1933); but at the same time we should not overlook its morphological constitution by saying that its configuration is determined by physiological factors. As shown above, the ovarial cavities do not originate in a haphazard manner; but a spiral sequence and co-ordination are met with in their origin such as to justify the existence of a fundamental ground-plan in floral organisation. By saying that the gynoeceium is constituted of three carpellary leaves, it is not presumed that the three leaves originate as separate entities and fuse at the margins in the course of development. But, according to the trimerous tendency inherent in the receptacle, they originate in co-ordination and grow up as a consolidated morphological entity. One important modification of the monomorphic view of carpels is the recognition that in an epigynous flower the pedicel below the ovary consists of both axis and ovary wall, as shown by the course of the vascular bundles. During development of the ovary as a composite organ, the axis tissue lines the outer part of the carpellary leaves to give the gynoeceium the appearance of a receptacular crater, which is the necessary outcome of the configuration of the floral members in an epigynous flower. The evidence for this view is taken not only from vascular anatomy, but also from the disposition of the cell layers in the ovary wall. Fig. 7 shows the longitudinal course of the vascular bundles along the ovarial wall. It is clear that the pedicel bundle is not giving a branch to the ovarial wall, but it bends outwards and continues as the bundle of the ovary wall. Again, anatomically the number of cell layers in the ovary wall outside the vascular strands is more than that which is required if the ovary is merely a carpellary



structure. On this point Saunders (1925) says that 'if in the thickness of the wall, there are no more than two cell-layers external to the vascular cords, no part of this containing wall can be composed of axis tissue'. In *Elettaria*, however, there are many wall layers outside the vascular cords, some of which must belong to the axis. This fact, together with the evidence from vascular anatomy, points to the conclusion that the inferior ovary is not merely a carpellary leaf modification, but that the axis tissue is also fused with the walls of the ovary to give it the appearance of a receptacular crater.

In saying this, it is not intended to interpret the gynoeceium as a 'Phylloclade', as McLean Thompson (1929) has suggested for the Legume. According to the Phylloclade view, the ventral suture tissue of the legume bearing the two rows of ovules is partly axial and partly foliar. But Newman (1933) has shown that the ovules in *Acacia Baileyana* are borne in two series on the margins of a carpellary leaf, and that no part of the ovule-bearing tissue is axial. Newman argues that if the bundles supplying the ovules are also partly axial, they would extend into the style; but he finds on the contrary that they end at its base. In *Elettaria*, also, the bundles supplying the ovules terminate in the inner staminal whorl without extending into the style, and the three bundles in the latter are only branches of the median bundles of the peripheral groups. There are, therefore, no axial bundles extending into the style. Payer (1857) has shown in *Alpinia nutans* that the central tissue bearing the ovules is produced developmentally by the ingrowth of three twisted 'cordons', which proves that the central tissue bearing the ovules is the growth-product of the carpellary leaf-margins only and is not the axial tissue. When the tissue bearing the ovules is thus shown to be essentially foliar in structure, the ovules must necessarily be of foliar origin. But unlike *Acacia*, which has a superior gynoeceium, the inferior ovary of *Elettaria* has the axis tissue also incorporated in its wall. The ovary wall is, therefore, composed of an outer layer which is a continuation of the axis and an inner layer which is formed from the carpels. The appearance of a receptacular crater is thus the result of the ovary being inferior. The back-to-back disposition of the ovules in each loculus of the ovary also supports the essential foliar constitution of the gynoeceium.

#### *Development of the ovule.*

The development of the ovule was traced from the inception of the ovular projection to the formation of the embryo-sac. The ovules are arranged in two series in each loculus on the central tissue formed by the fusion of the carpel margins. The stages in the development of an ovule, with its disposition in relation to the loculus of the ovary, are shown in Pl. 11.

The ovules originate as a papillate protrusion from the central tissue formed by the fusion of carpellary leaf margins (Pl. 11, a). The cells of this tissue are undifferentiated (f). At a slightly later stage, the ovule begins to show a prominent hypodermal cell by its increase in size as well as its rich contents (c).

The beginnings of the outer integument are visible at this stage as two cells, being pushed out from the general surface on either side. A periclinal wall then divides the hypodermal initial cell into an outer (the primary wall cell) and an inner (the primary sporogenous cell) as shown in *d*. A little later the outer cell appears to be pushed to the exterior by the increased growth of the inner cell (*e*). Two outer cells are then formed by an anticlinal wall in the primary wall cell, *f*. This is significant, inasmuch as it minimises the distance which the pollen tube has to traverse before reaching the embryo sac, besides facilitating the construction of a canal by their separation during fertilization. The primary sporogenous cell grows rapidly, and without further division functions directly as the megaspore mother cell (Pl. 11, *f*). *g* is an enlarged drawing of the mother cell showing the early prophase stage before its division into a tetrad. By this time the inner integument has grown considerably, while the outer one is seen only as two small projections on either side of the chalazal region of the ovule (*i*). The megaspore mother cell now undergoes two successive divisions accompanied by reduction to form the linear tetrad (*j*). The outer integument has by this time grown up considerably.

The functional megaspore is the lowest of the group. This cell grows rapidly, disorganising the sister cells above in order of proximity, and it functions ultimately as the megaspore. Pl. 11, *k*, shows the stage at which the megaspore has destroyed the one just above and the one still above is in the process of disintegration. A further stage of disorganisation and the consequent development of the megaspore are shown in *l*. In the next stage (*m*) the uninucleate embryo sac is seen, and the two integuments are now overlapping the nucellus. This is followed by free-nuclear division to give rise first to the binucleate and still later to the eight-nucleate embryo sac (*n* & *o*). Meanwhile, the inner integument has grown towards the upper region of the nucellus, forming a wide tubular micropyle. During the development outlined above, there has been a gradual bending at the chalazal region to give rise ultimately to semi-anatropous disposition of the two series of ovules. Their back-to-back arrangement in each loculus (*p*) is worthy of special note.

One or two points require a brief discussion. The development of the ovule has been a favourite subject of investigation in the past. Among recent investigators the names of Cooper in *Bougainvillaea* (1931 and 1932) and in *Melilotus* (1933), Reeves (1930) in *Alfalfa*, and Newman (1933) in *Acacia*, may be mentioned. In the details of development of the ovules of *Elettaria*, there are no appreciable variations from the general plan. The two integuments characteristic of the Monocotyledons are present, though *Crinum* is often recorded as an exception to this. The single-celled archesporium is found here also as in other Monocotyledons, the recorded exception being *Ornithogalum pyrenaicum* (Guignard, 1882), where two archesporial cells were noted. Though the anticlinal division of the primary wall cell was observed by several investigators, its significance in relation to the growth of the pollen tube has not been

suggested before. This division, which increases the cells without thereby adding to the wall layers, naturally minimises the resistance to be encountered by the pollen tube in its course to the embryo sac.

Finally, there remains the question of the morphological nature of the ovules and its bearing on the interpretation of the gynoeceum. According to the carpellary theory, the ovule is a transformed leaf-bud at the margins of the carpellary leaves, as in the well-known case of *Bryophyllum*. The supporters of this view are Van Tieghem (1869), Warming (1877), and several others. When cauline ovules came to be noticed, Endlicher and others regarded them as cauline rather than foliar in origin. More recently the ovules have been interpreted as terminal structures of branch systems, and the Angiospermic flower—at least the primitive *Populus* type—is regarded as being derived from seed-bearing inflorescences of the *Corystospermaceae* by postulating the fusion of the cupules to form the ovarial cavity and the aggregation and subsequent fusion at the apex of a branch of a number of microspore- and megaspore-bearing appendages. This view is advocated by H. Thomas (1933), and, though it is applicable to some extent in deriving the Amentiferous type of flower, he himself admits that it is not applicable to certain types of advanced flowers. ‘The usual interpretation of the flower as corresponding to a bud composed of an axis with lateral members seems to be unassailable in the case of certain flowers, but I trust that my suggestion of another origin of certain simple unisexual flowers is not unreasonable.’

This observation assumes a polyphyletic origin for the Angiosperms, which is in harmony with the opinion of Hagerup (1934) and other recent writers. As a result of the present investigation in the *Elettaria* flower, I am inclined to the view that the unitary bud character of the flower seems to be fairly unassailable. The co-ordination of the ovarial and stylar cavities, the spiral sequence in the origin and termination of the former, the regularity in the course and disposition of the vascular strands in harmony with a fundamental ground-plan, all suggest that the flower as a whole is the result of the co-ordinated development of a shoot with the floral members appearing in spiral series like the foliage leaves. The spiral origin of the parts of the flower and the foliar nature of the carpels demonstrated here supports the theory that the flower is essentially a metamorphosed shoot. Zimmermann (1930) describes this similarity as parallel formation (‘Die Gesamtsporangienstände, die Blüten, sind parallelbildungen zu den vegetativen Sprossen . . .’). In this connexion Rendle (1933) has stated that whatever may have been their origin, and which ever may be regarded as the parent form, surely the floral and foliage leaves have a common morphological value.

Scott (1933) suggested that the old carpellary view, so well restated by Goebel in his ‘Organography’, will probably continue to hold the field until more definite evidence can be brought against it. In Pl. 11, *p*, the cross-section of the mature ovary is shown with the back-to-back disposition of the ovules

in each loculus. This is the only natural disposition one would expect, if the ovules are regarded as borne on the infolded margins of the carpellary leaves, and the facts of anatomy support this.

#### SECTION B.—CYTOLOGY.

The cytology of *Elettaria*—even of Zingiberaceae—has received very little attention.

In the cell-composition of the plant body, the occurrence of certain big cells in all the tissues is noteworthy. They are most abundant in the perianth, and Pl. 12, fig. 3 shows one such cell with the adjoining cells. It has abundant cell-contents with a conspicuous nucleus. From a comparison of the size relation with adjoining cells, it seems that it may be a polyploid cell, but the chromosome number could not be obtained as no divisions of this cell were seen. The general anatomical features indicate that they serve some physiological function in connexion with the secretion of some aromatic substance. Polyploid cells in animal tissues have been recorded by Frolova (1929) in the rectal glands and fat-bodies of *Pegomyia geniculata*.

##### *The cell-contents and chromosome number.*

The only result so far recorded on the cytology of Zingiberaceae has been the ascertainment of the chromosome number of two species—*Zingiber officinale*,  $2n=22$  (Sugiura, 1928), and *Z. mioga*,  $2n=55?$  (Morinaga, 1929). As a result of the present investigation, the chromosome number of *Elettaria* has been determined from the somatic cells of the root-tip and corroborated by the number in the meiotic divisions. The  $2n$  number is 48, and a metaphase plate of the same is shown in Pl. 12, fig. 2. This number was confirmed by counts of several metaphase plates as well as from late stages of prophase (Pl. 12, fig. 1). Decisive confirmation was obtained by counts of several heterotypic metaphase plates, where 24 bivalents were observed in all cases (Pl. 13, fig. 18).

The somatic chromosomes are more or less of the same size, with median or sub-median constriction. Owing to their extreme smallness, very little work regarding their structure and behaviour in mitosis has been possible. The numbers of two more species of Zingiberaceae were ascertained with a view to comparing their size-relation with those of *Elettaria*—*Hedychium Elwesi*,  $2n=66$ , and *Costus malarotiensis*,  $2n=18$ . Two metaphase plates from the root-tips of these are shown in Pl. 12, figs. 6 & 5 respectively. The three metaphase plates (Pl. 12, figs. 2, 5, & 6) are drawn on the same scale, and a comparison of the size-relations of their chromosomes leads to the conclusion that the size of the chromosomes in related genera decreases with increase of number, or *vice versa*. Thus, of the three species under consideration, *Costus malarotiensis* has the biggest chromosomes and the smallest number, while *Hedychium Elwesi* has the smallest chromosomes and the largest number, *Elettaria Cardamomum* occupying an intermediate position both in relation to number and size,

Such a relationship between number and size of chromosomes in related genera has been reported by Davie (1933) in the Malvaceae.

### *Microsporogenesis.*

A detailed study of the meiotic divisions leading to microsporogenesis was made, as the material offered exceptionally large pollen mother-cells.

A cross-section of a fertile anther at the microspore mother-cell stage is shown in Pl. 12, fig. 4. It shows a distinctly bilocular anther, each loculus being further subdivided, giving ultimately four microsporangial cavities. One sac is shown on a magnified scale in Pl. 12, fig. 7. A significant peculiarity noted here is the inpushing of the tapetal cells into the microsporangial cavity and the occasional binucleate nature of some of the tapetal cells as shown in figs. 9 and 10 below. Smith (1898) in Pontederiaceae and Caldwell (1899) in *Lemna* have recorded the wedging in of the tapetal cells into the cavity. Binucleate condition of the tapetal cells in *Typha* (Schaffner, 1897) and in many other forms and the trinucleate condition in *Hepatica* (Coulter, 1898) have been reported.

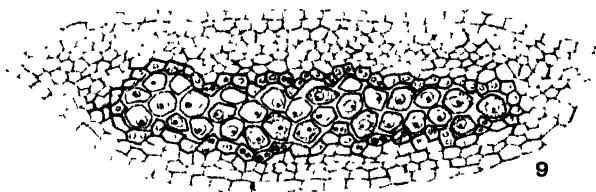


FIG. 9.—Longitudinal section of the anther showing the inpushing of the tapetal cells into the sporangial cavity.  $\times 300$ .

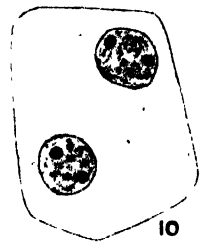


FIG. 10.—Binucleate tapetal cell.  $\times 1500$ .

In the resting stage the microspore mother-cells are well spaced in the sporangial cavity. They are often hexagonal (Pl. 12, fig. 7), the wall is very thin, and the cytoplasm is rather dense and granular. The nucleus generally occupies the central position in the cell, and is more or less spherical (Pl. 12, fig. 8). The nucleolus stains easily and very deeply with gentian violet. In size it is exceptionally large and it usually shows small spherical buds. No rod-shaped budding of the nucleolus simulating chromosomes was observed as reported by Heimlich (1928) in *Cucumis sativus*. The chromatin shows fine threads loosely distributed in the nuclear cavity. At the end of the resting stage, the cells grow and begin to lose their hexagonal shape. Due to the growth of the sporangial cavity the mother-cells are well spaced at this time.

### *Heterotypic division.*

At the very early stage of heterotypic prophase, the microspore mother-cells take a more or less oblong or oval shape with rounded corners (Pl. 12, fig. 9). The nucleus is very often located towards one side of the cell. Early prophase

leptotene threads are seen to be made up of two chromonemata twisted together giving at some regions a beaded appearance. This appearance has often been interpreted as chromomeres and the thread at the leptotene stage was considered to be single. But in the present material the leptotene thread is seen to be double with the components twisted round each other, giving a chromomeric appearance at the regions where the diamond areas formed by the twisted thread retain more stain.

At the mid-prophase stage a synizetic contraction was observed in several cases, during which the leptotene threads become massed together into a more or less dense knot, usually situated towards one side of the nuclear cavity and often enclosing the nucleolus (Pl. 12, fig. 11). After synizesis the dual twisted threads associate in pairs. The pairing homologues have greater affinity at the ends. A peculiarity noted here was that the two ends of the pairing homologues do not join simultaneously, but one end approaches its partner before the two other ends meet. Different stages of this type of pairing are shown in Pl. 12, fig. 13, where a cell is drawn with only four pairs of homologues to avoid confusion, and the pairs are further analysed in Pl. 12, fig. 14. So much is certain, that there is more affinity at the ends and the degree of parallel association depends upon the affinity of the pairing homologues. This observation is in agreement with that of Hedayetullah (1933) in *Oenothera missouriensis*.

The pairing homologues contract through the remaining stages of the prophase, and assume the maximum contraction at metaphase. During these stages the threads assume various configurations, sometimes lying one over the other and crossing at other regions to give the appearance of chiasmata. The configurations of the twenty-four bivalents are seen in early diakinesis in Pl. 13, fig. 15. At this time the nucleolus gradually diminishes in size and the nuclear membrane slowly disintegrates. A stage of this process is shown on a magnified scale in Pl. 13, fig. 16. Following the disappearance of the nuclear membrane the paired bivalents arrange themselves on the metaphase plate.

During these stages the cell wall has become so very thin that it seems to disappear, with the result that at metaphase the cell has a more or less irregular shape (Pl. 13, fig. 17). The twenty-four pairs of chromosomes are shown in Pl. 13, fig. 18. Even from the very early metaphase the bipolar nature of the spindle is evident, and soon the bivalents arrange themselves at the equatorial region of the spindle (Pl. 13, fig. 19). These bivalents are analysed in fig. 20. A feature of the heterotypic spindle is the highly pointed nature of its poles.

At the early anaphase stage the halves of each bivalent move to opposite poles. All the chromosomes do not move together, but lagging of chromosomes was observed during anaphasic separation. Three stages of this separation are shown in Pl. 13, figs. 21, 22, & 23, where twenty-four univalents are seen on either side, thereby establishing the reduced haploid number of chromosomes in each daughter nucleus.

As the chromosomes reach the poles, signs of thickening are visible at the equatorial region of the spindle (fig. 24). This is the first indication of the

cell-plate. The chromosomes on reaching the poles mass closely to form the telophase nucleus. As they are exceptionally small at this stage, nothing could be made out about their structure. Nuclear membranes soon enclose the developing daughter nuclei (fig. 24) and interkinesis follows.

During interkinesis the daughter nuclei are approximately hemispherical, but somewhat concave on the anti-polar sides. Nucleoli also make their appearance at this time in each daughter nucleus. At this stage a broadening of the diameter of the spindle is seen at the equatorial region, due to the approach of the daughter nuclei. A clear line is now visible across the equatorial thickening, simulating a longitudinal split of the plate (fig. 25).

*Homoeotypic division and formation of microspores.*

The second division occurs in the daughter nuclei in the usual manner, to give rise to the tetrad nuclei (figs. 26 & 27). The spindles are not clearly differentiated here as in the heterotypic division. One significant feature noted in the formation of the tetrad is that the four microspores are formed in the same plane, and not in the more usual tetrahedral manner (fig. 28). In the formation of the microspores, successive division was noted as in other Monocotyledons, and not simultaneous division as is characteristic of Dicotyledons. The quadrants of the tetrad gradually assume a reniform shape by the outer wall contracting centripetally.

DISCUSSION.

The first problem to be discussed is the duality of the leptotene threads and their chromomeric appearance. The chromomere theory, which postulates certain granules as forming an integral part of chromosomes, was propounded by Pfitzner in 1880. These granules were first called 'Pfitzner's granules'. Many investigators have reported the presence of such granules in the prophase stages of mitosis and meiosis of both plants and animals. Some of the most important of them are Strasburger (1907 and 1911), Digby (1912) in *Primula*, Wenrich (1916) in *Phrynotettix*, Sands (1923) in *Tradescantia*, and Belling (1928) in Liliaceous plants. Belling even went to the extent of ascertaining the numbers of these chromomeric granules. Among recent investigators, Hedayetullah (1931) in *Narcissus* and Perry (1932) in *Galanthus*, have observed and figured chromomeric structures in certain prophase and telophase stages of mitosis.

Others hold the view that the chromomeres are not structural units of chromosomes, but are mainly a misinterpretation of the peculiar structural aspect of the chromosomes in the prophase stages. Some of the most important of these observers are Martins Mano (1904), Grégoire (1906), Sharp (1913), and Bolles Lee (1920). Among recent investigators, the names of Smith (1932) in *Galtonia*, O'Mara (1933) on the generative nucleus of *Lilium*, and Koshy (1933) on the somatic chromosomes of *Allium* may be mentioned. All these observers deny the existence of such morphological units in the constitution of the chromosomes, and give several interpretations of the chromomeric appearance. Some say that they are due to the twists and bulges of the twisted

chromonema, while others attribute the appearance to an optical effect due to the crests of twists being in sharp focus.

Consequently, the present material was examined with great care, and I have come to the conclusion that the so-called 'chromomeres' are not structural units of the chromosomes, but are only the appearances of the interlaced leptotene threads under the microscope. In lightly stained preparations it was possible to see the twisted thread, while in deeply stained preparations the same stage showed a beaded appearance, due to the stain being retained in the diamond areas formed by the twisted threads. As Sharp (1929) has pointed out, these interpreted chromomeric granules are far too few to meet the genetical requirements.

In the somatic cycle of chromosomes, splitting at the prophase of the division previous to the one at which the halves separate has been demonstrated by Sharp (1929) in large somatic chromosomes and by Kaufmann (1926) in *Tradescantia pilosa*. A persistent interlacing aspect for chromosomes in all stages of the mitotic cycle has been claimed by Eichhorn (1931) from his study of living materials, and Koshy (1933) in *Allium*. In the premeiotic division of Dipteran chromosomes, duality has been demonstrated in the telophase by McClung (1928) and Robertson (1931). From this one would expect that the heterotypic prophase chromosomes should be dual twisted threads, and the evidence of leptotene duality from the present material is in complete harmony with expectation. Moreover, indubitable evidence of leptotene duality has been obtained by some recent investigators, e.g., Kaufmann (1931) in *Tradescantia pilosa* and Smith (1932) in *Galtonia*. Newton (1927) figures the leptotene threads of *Tulipa* with a clear indication of twisting.

The early prophase leptotene threads are dual and twisted, and not single as Darlington (1931) assumes in his precocity hypothesis. According to his view, the supposed distinction between mitosis and meiosis is a delay in the prophase split in the heterotypic division of meiosis, the early leptotene thread being single. But the duality of the leptotene thread demonstrated and discussed above removes this supposed distinction between mitosis and meiosis, and shows that the essential difference between the two is only a complete suppression of the prophase split in the latter. When the leptotene duality is considered in conjunction with the prophasic chromomeric appearance, the following alternative suggests itself: either the leptotene threads are single with chromomeres or they are double without chromomeres. The evidence from this investigation is in support of the latter proposition, namely, leptotene duality and the absence of the so-called chromomeres.

The question of the mode of pairing of the homologues has been a subject of much controversy. This matter was examined in detail in the present material and it was found that the pairing homologues had greater affinity at one end to begin with and later on they assume a more or less parallel disposition, leading ultimately to the association of the other end as well (Pl. 12, fig. 14).



Finally, there remains the consideration of the mode of cytokinesis and the formation of the reniform microspores. Regarding cytokinesis, there are two methods entirely different in general aspect from one another, viz. by furrowing or constriction and by the formation of cell-plates. Broadly speaking, cleavage by constriction is characteristic of mitosis in higher animals. But in plants, also, this method is recorded in the quadripartition of microspores by Farr (1918, 1922) in *Magnolia* and *Nelumbo*, Castetter (1925 and 1926) in *Melilotus* and *Cucurbita*, Weinstein (1926) in *Phaseolus*, Gates (1927) in *Lathraea*, Janaki Ammal (1932) in *Nicandra*, and by many others. The second method, by cell-plate formation, is the most common type in plants. According to many earlier accounts (Strasburger, 1875, 1880; Allen, 1901), the cell-plate is formed by the fusion of swellings at the equatorial region of the spindle, the plate then splitting to form the plasma membranes of the daughter protoplasts, the primary wall layer then being secreted between them. Robyns (1929) and Bělař (1929) have recently shown that the cell-plate first appears as a continuous film and not as a series of swellings or granules. More recently, Becker (1932) observed in living material of the staminal hairs of *Tradescantia* that the cell-plate material appears first in the form of minute droplets, which then unite to form a continuous plate; and he argues that there is a local dissociation—'Entmischung'—of two phases, one of these forming the cell-plate, while the other remains as the plasma membrane.

The cleavage process in the present material is by the cell-plate method. Towards the end of the late telophase following the reconstruction of the daughter nuclei, a hyaline layer is seen at the equatorial region of the spindle (Pl. 13, fig. 24). From the hyaline nature of this layer, it is to be presumed that the earlier elements of the cell-plate are of fluid nature, as Bělař and Becker have found. Then a clear region is seen along this hyaline layer, simulating a longitudinal split as shown in Pl. 13, fig. 25. Since the microspores have to separate later, unlike somatic daughter cells, no middle lamella is secreted in the clear region as assumed by previous accounts; but, on the other hand, the walls increase in thickness by further depositions towards the inside from the cytoplasm, as observed by Gates (1924) in *Lathraea*. The spines of the mature microspores are very conspicuous (Pl. 13, fig. 30), and their early appearance, even when the spores are within the mother-cell wall (Pl. 13, fig. 29), suggests that they are formed under control of the protoplast inside. It is also worthy of note that *Elettaria* pollen-grains are almost the only recorded instance of spiny microspores in Monocotyledons.

#### SUMMARY AND CONCLUSIONS.

The inflorescence of *Elettaria Cardamomum* is described, and the fact that the flowers are in groups of three or occasionally four with one much older than the others.

The morphological nature of the labellum is worked out with special reference to the course, number, and disposition of the vascular bundles. The morphological entity called the labellum is a composite structure having in its constitution members of both the staminal whorls; being composed of the anterior member of the outer whorl and the two antero-laterals of the inner whorl. The floral diagram is consequently amended.

The two tooth-like structures,  $x$  &  $y$  (fig. 3 ZZ), are demonstrated to be glands with little or no morphological value, and the recent claim that they are staminodes or stylodes is shown to be untenable.

The gynoecium is essentially foliar in constitution, being formed by the co-ordinated development of three carpellary leaves with the axis tissue lining the outside of the ovary wall in the inferior ovary to give it the appearance of a receptacular crater.

It is shown that, while floral organs may vary in external form to some extent with reference to physiological and biological requirements, the essential trimerous ground-plan of the Monocotyledons is well preserved in the floral constitution of *Elettaria*.

The development of the ovule is traced in detail from the inception of the ovular projection to the formation of the embryo-sac, and the significance of the anticlinal division in the initial wall-cell in connexion with the passage of the pollen-tube is suggested.

The presence of isolated gigantic cells, possibly polyploid, is recorded, and their function as glands in the secretion of aromatic oils, so characteristic of the members of this family, is suggested.

The chromosome number of *Elettaria Cardamomum* is  $2n=48$ , from the root-tip cells, and corroborated by counts in the meiotic division. The chromosome numbers of two more species of related genera are ascertained for the first time. They are :—

*Costus malarotiensis* . . . . .  $2n=18$ .

*Hedychium Elwesi* . . . . .  $2n=66$ .

A comparison of the relation of size and number of the somatic chromosomes in these three related genera yields the conclusion that the size increases with decreasing number or *vice versa*.

Microsporogenesis is traced in detail in *Elettaria*, with special reference to early stages of meiosis.

The duality of the leptotene threads is demonstrated and discussed with special reference to the chromomeric appearances reported by earlier workers in the early stages of mitosis and meiosis. The so-called 'chromomeres' are the misinterpreted images of the twisted aspect of the early leptotene threads, under different degrees of staining. This leptotene duality is taken in conjunction with their reported singleness as assumed by the precocity hypothesis and discussed to show that the essential difference between mitosis and meiosis

is *not a delay* in the prophase split in the latter, as assumed by the above hypothesis, but a *complete suppression* of the prophase split in the first division of meiosis.

The pairing of the homologues is shown to begin at one end and gradually proceed to the other end.

The mode of cytokinesis in tetrad formation is by the cell-plate method, and the cells of the tetrads are often arranged in one plane and not in the tetrahedral form.

The reniform microspores are formed by a centripetal contraction in each quadrant in the early stage of their development. The presence of spiny pollen-grains is observed and suggested as the only recorded instance of such spiny microspores in Monocotyledons.

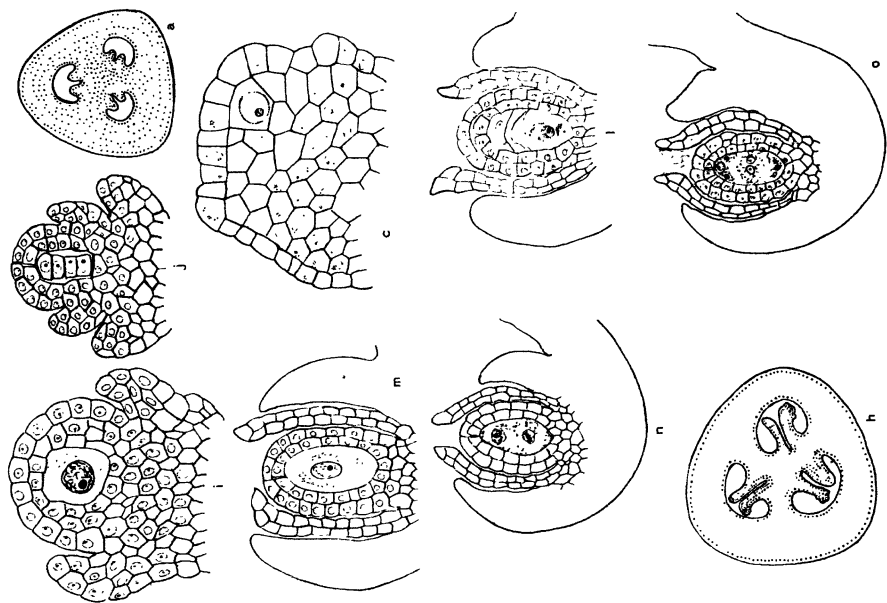
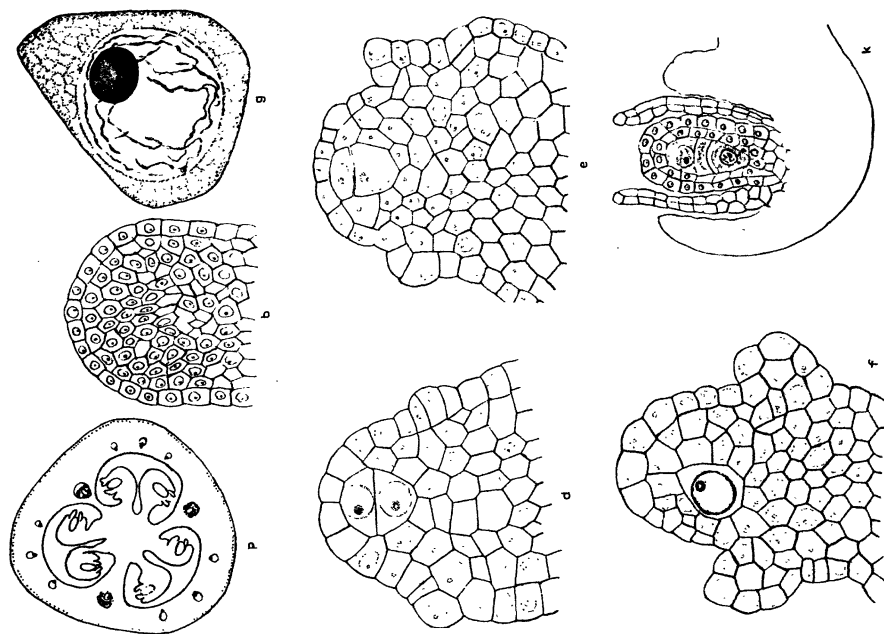
Finally, I wish to express my most sincere thanks to Prof. R. Ruggles Gates, F.R.S., for the kind guidance, valuable suggestions, and helpful criticisms throughout the progress of this investigation.

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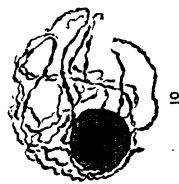
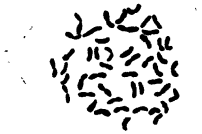
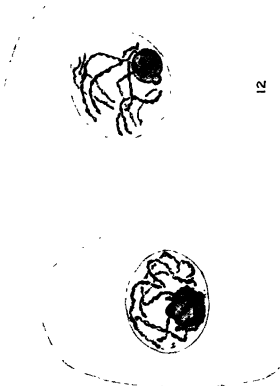
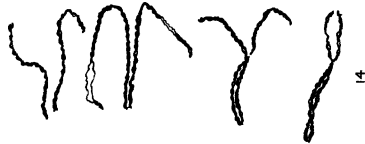
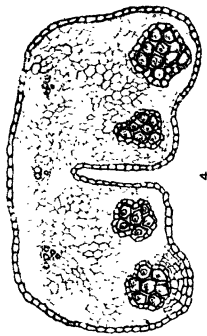
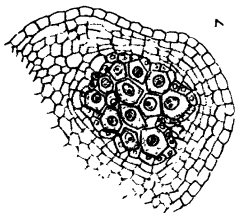
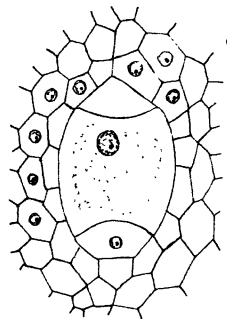
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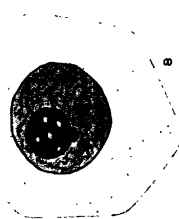
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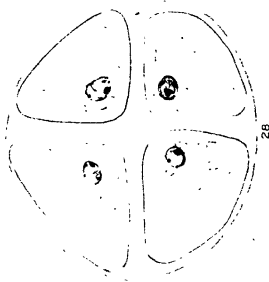
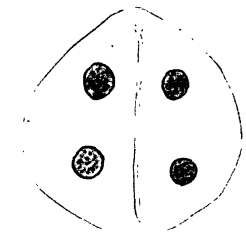
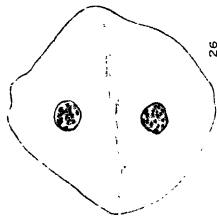
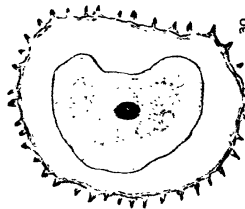
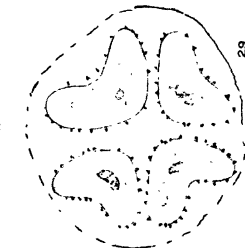
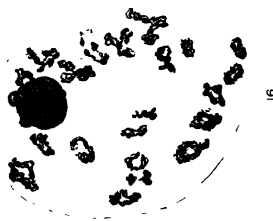
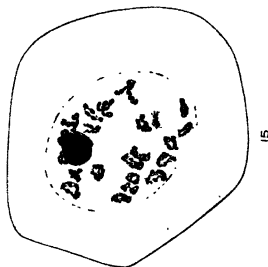


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ELETTARIA

CARDAMOMUM MATON



## ELETTARIA

**CARDAMOMUM MATON**





- d. Periclinal division of the hypodermal initial cell to give rise to an outer (primary wall cell) and an inner (primary sporogenous cell).  $\times 1500$ .
- e. The primary sporogenous cell grows and the primary wall cell appears to be smaller.  $\times 1500$ .
- f. Formation of two wall-cells by the anticlinal division of the primary wall cell. The primary sporogenous cell grows in size to form the megaspore mother-cell.  $\times 1500$ .
- g. Megaspore mother-cell in prophase stage.  $\times 3400$ .
- h. General nature of the ovary at this stage and the disposition of the ovules in each loculus of the ovary.  $\times 60$ .
- i. Megaspore mother-cell with the two wall layers. Note the origin of the outer integument at this stage. The inner integument, which started in stage C, has now grown considerably.  $\times 800$ .
- j. The linear tetrad stage with the two integuments developing on either side.  $\times 800$ .
- k. Growth of the lowest of the tetrad, disorganizing the upper ones in order of proximity.  $\times 800$ .
- l. A later stage of disorganization of the sister cells and the further growth of the lowest megaspore.  $\times 800$ .
- m. Uninucleate embryo-sac with the integuments advancing to form the micropyle.  $\times 800$ .
- n. Binucleate stage of the embryo-sac.  $\times 800$ .
- o. Final 8-nucleate embryo-sac showing the wide tubular micropyle.  $\times 800$ .
- p. General nature of the ovary at this stage, showing the back-to-back disposition of the semi-anatropous ovules in each loculus.  $\times 60$ .

#### PLATE 12.

- Fig. 1. Late prophase stage of somatic division from the root-tip cell of *Elettaria*.  $\times 2500$ .
- Fig. 2. Metaphase plate of somatic division of *Elettaria* showing 48 chromosomes.  $\times 2500$ .
- Fig. 3. Gigantic glandular cells, possibly polyploid, from the perianth, with the adjoining cells to show their size relation.  $\times 800$ .
- Fig. 4. Cross-section of the anther showing its bilobed quadrilocular nature.  $\times 250$ .
- Fig. 5. Somatic metaphase plate from a root-tip cell of *Costus malarotiensis* showing 18 chromosomes.  $\times 2500$ .
- Fig. 6. Somatic metaphase from a root-tip cell of *Hedychium Elaeagni* showing 66 chromosomes.  $\times 2500$ .
- Fig. 7. One loculus of the anther enlarged to show the closely packed pollen mother-cells and the impushing of the tapetal cells into the sporangial cavity.  $\times 400$ .
- Fig. 8. Resting pollen mother-cells with distinct angular corners.  $\times 1000$ .
- Fig. 9. Heterotypic prophase stage of the pollen mother-cell showing the twisted leptotene threads having at some regions a chromomeric appearance.  $\times 1000$ .
- Fig. 10. Nucleus of the same stage, enlarged to show the twisted nature of early leptotene threads.  $\times 1500$ .
- Fig. 11. Synizetic contraction stage.  $\times 1000$ .
- Fig. 12. Cell showing the nucleus with four pairing homologues represented. Note the 'budding' of the nucleolus.  $\times 1000$ .
- Fig. 13. Pollen mother-cell showing the pairing homologues coming together with greater affinity at the ends. Note one end of each homologue approaching its partner earlier than the other two ends.  $\times 1000$ .
- Fig. 14. Four pairing homologues of the above nucleus, enlarged to illustrate the mode of pairing.  $\times 2500$ .

## PLATE 13.

- Fig. 15. Early diakinesis stage showing the paired bivalents (24 in number) highly contracted. Note the gradual disappearance of the nuclear membrane.  $\times 1500$ .
- Fig. 16. Same stage as above, enlarged to show the disintegration of the nuclear membrane.  $\times 1000$ .
- Fig. 17. Heterotypic metaphase plate showing the 24 bivalents in polar view. Note that the cell-wall has become very thin.  $\times 1000$ .
- Fig. 18. The bivalents of the heterotypic metaphase plate, enlarged.  $\times 1500$ .
- Fig. 19. Side view of the heterotypic metaphase plate showing the bivalents arranged at the equatorial region of a distinctly bipolar spindle.  $\times 1500$ .
- Fig. 20. Metaphase chromosomes analysed in side-view.  $\times 2500$ .
- Fig. 21. Early anaphase of heterotypic division showing 24 univalents passing to each pole. Note the lagging of chromosomes and the pointed spindle.  $\times 2500$ .
- Fig. 22. Side-view of late anaphase. Note the thickening at the equatorial region of the spindle.  $\times 2500$ .
- Fig. 23. Slightly oblique view of late anaphase.  $\times 1500$ .
- Fig. 24. Early telophase of heterotypic division.  $\times 1500$ .
- Fig. 25. Late telophase nuclei with a clear region across the equatorial thickening, simulating a split.  $\times 1500$ .
- Fig. 26. The two daughter cells after the first division.  $\times 800$ .
- Fig. 27. Tetrad nuclei after the second division.  $\times 800$ .
- Fig. 28. The tetrads arranged in one plane within the mother-cell wall.  $\times 800$ .
- Fig. 29. Tetrad of microspores. Their reniform shape appears to be due to a centripetal contraction in each. Note the presence of spines on the young microspores, even when they are within the mother-cell wall.  $\times 800$ .
- Fig. 30. Mature pollen grain with distinct spines.  $\times 800$ .



The limnology of the Long Pool, Butterby Marsh, Durham: an account of the temperature, oxygen-content, and composition of the water, and of the periodicity and distribution of the phyto- and zooplankton. By BENJAMIN MILLARD GRIFFITHS, D.Sc., F.L.S.

(With 5 Text-figures)

[Read 7 November 1935]

# INTRODUCTION.

The Long Pool lies at the upper end of Butterby Marsh, Durham (Griffiths, 10). It occupies part of the old channel of the River Wear, and has existed in its

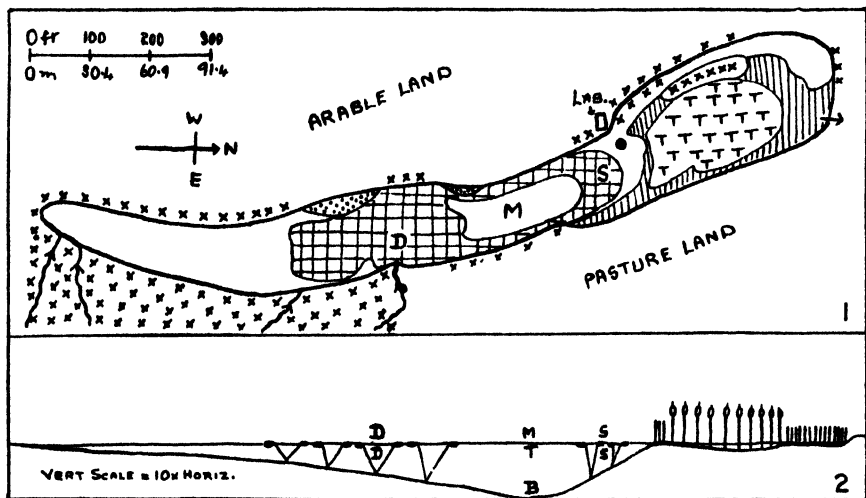


FIG. 1.—MAP OF LONG POOL AND TYPHA MARSH: x x x, deciduous trees; dotted areas, *Phragmites communis*; rectangular cross-hatching, *Nuphar luteum*; parallel lines, *Rumex hydrolapathum*; T T T T, *Typha latifolia*; black circle, *Scirpus lacustris*; M, S, D, collecting stations.

FIG. 2.—MEDIAN VERTICAL SECTION OF ABOVE: vertical scale 10×horizontal scale. D, M, T, B, S, collecting stations.

present form since 1820. It is a self-contained habitat, deriving the whole of its water supply from the adjacent deciduous woodland, pasture, and arable land, an area of 120 acres (48.56 hectares). The pool is 900 ft. long, 90 ft. wide (274 m.×27.4 m.), 2.27 acres in area (0.91 hectares), and reaches a depth of 10 ft. (3.0 m.) over a considerable area at its northern end (see figs. 1 & 2).

The basin of the pool lies in the sandy clay and clay silt of a former glacial lake bed, but the original floor is everywhere overlain by a deposit from 9 in. to 2 ft. thick (22·8 to 60·9 cm.) of autochthonous organic detritus, consisting of finely divided black particles (black mud, muck, faulschlamm) forming the soil in which the aquatic vegetation is rooted. The detritus is inhabited by Chironomid and other larvae, worms, leeches, Cyprids, *Pisidium*, and the lime-sulphur bacillus *Achromatium oxaliferum* (*Hillhousea mirabilis*) and the sulphur bacillus *Beggiatoa alba*.

The water of the pool is nearly neutral, pH 7·9–7·5, but the inflowing water of the chief drainage channel has a pH of 8·0. Dissolved solid matter amounts to 40 to 50 parts per 100,000. A Secchi disk is just visible at ten feet during unusually bright calm periods, but is seldom visible below eight or nine feet, and in dull windy weather may be invisible at four or five feet. The general limit of visibility coincides fairly closely with the limit of the macrophytic vegetation, which does not extend below eight feet.

The long sides of the pool are steep at the north end, but are less steep at the south end. The south end is much shaded by trees (see fig. 1), but the north end is open. The littoral marsh vegetation is scanty owing to the steepness of the banks at the north end, and possibly owing to the shade of the trees at the south end. The vegetation (see figs. 1 & 2) comprises two societies of *Phragmites communis*, one small society of *Scirpus lacustris*, and a number of small and broken groups of *Carex paludosa*, *Digraphis arundinacea*, *Rumex hydrolapathum*, *Equisetum limosum*, *Sparganium ramosum*, and *Alisma plantago*. At the north end, the pool is bounded by a marsh-formation of *Typha latifolia* and *Rumex hydrolapathum*.

The aquatic vegetation consists of an almost pure society of *Nuphar luteum*, covering the floor from 2 ft. 6 in. to 7 ft. 6 in. (0·76 m. to 2·28 m.), and leaving an area of about 0·25 acres (0·1 hectares) of open water in the centre of the north end of the pool. A little *Potamogeton pusillus* occurs in the outer edges of the *Nuphar* society, but the rest of the floor of the pool, both in the centre and at the north and south ends, is bare of rooted aquatic plants.

#### THE TEMPERATURE.

From February 1929 to December 1931 observations were made of the temperature of the water at a point six inches below the surface in the middle of the open water (T, fig. 2), and at one foot off the bottom at a depth of nine feet (B, fig. 2) immediately beneath the point T. The temperatures were taken (and the plankton collections were made) by sending down a plankton-collecting jar, 750 c.c. in capacity, attached to the intake pipe of a plankton-pump of 1 litre capacity stroke. The end of the pipe within the jar was fitted with a cylindrical brass wire cage covered with no. 20 bolting-silk, and the brass cover of the jar was pierced with large holes. On pumping, water was drawn through the large holes into the jar, and through the bolting-silk strainer to the

pump and discharge-pipe. Fifteen litres of water were drawn through the apparatus, and the jar with its plankton catch and water-sample was hauled into the boat and the temperature of the sample taken. The weekly observations were made usually on a Tuesday at 3.0 p.m., but during November and December at 10.0 a.m.

A number of observations were made at various times of the temperature of the water at successive depths of one foot from top to bottom. It was found that when there was a difference between the top and bottom temperatures the fall was uniformly gradual, and that there was no sign of stratification.

In April 1932 consecutive daily observations were made of the top and bottom temperatures and of the strength of the wind as indicated by the agitation of the surface of the water. The results are shown in Table I.

TABLE I.

Date.	Wind.	Temperature.		Difference.
		Top.	Bottom.	
19. 4. 1932 . . . . .	No ripples.	7.9	7.3	0.6
20. 4. 1932 . . . . .	Strongly rippled.	8.5	8.5	0.0
21. 4. 1932 . . . . .	No ripples.	9.25	8.25	1.0
22. 4. 1932 . . . . .	No ripples.	9.25	8.25	1.0
23. 4. 1932 . . . . .	Strongly rippled.	8.5	8.5	0.0

The Table shows that the difference between the top and bottom temperatures is small even when there is no wind, and that complete uniformity of temperature is rapidly brought about by quite light breezes. It also shows that the temperature of the pool varies from day to day.

The weekly record of the top and bottom temperatures for the whole period of observation is given in Appendix 1.

In fig. 3 are plotted the average monthly temperatures, calculated from the weekly records, for the whole period of observation. By averaging the weekly records, minor fluctuations are smoothed out, and a general view is obtained of the temperature changes throughout the season.

Comparison of the above results shows that in this small and shallow pool there is no seasonal stratification of the water into an epilimnion and a hypolimnion, but that the temperature of the whole volume of water follows the seasonal atmospheric changes of temperature throughout the year. During the height of summer and in the depth of winter there is a slight tendency to stratify, but on any day the wind may be strong enough to disturb any incipient stratification and bring about uniformity of temperature from top to bottom. The effect of wind-action is clearly seen in Table I, where the temperature differences are small, but even when the temperature differences between the top and bottom are comparatively great, wind-action may prevent stratification and bring about uniformity of temperature from top to bottom. Thus, in the third week of June 1929, warm and calm weather brought about a difference of 2.0° C. between top and bottom temperatures, but a strong north-westerly gale in

the following week destroyed the incipient stratification and made the top and bottom temperatures uniform. A similar instance occurred in the third week of the following July when the difference was  $3.2^{\circ}\text{C}$ . In the winter, uniformity of top and bottom temperatures was common, partly owing to the greater windiness of the season and partly because the water is near its maximum density point and, therefore, easily upset. When the weather is windy the whole of the water may be reduced to a temperature below  $4.0^{\circ}\text{C}$ ., as for example in December 1929, when top and bottom was  $2.5^{\circ}$ ; January 1930,  $3.5^{\circ}$ ; February 1931,  $2.0^{\circ}$ . The bottom temperature fell below  $4^{\circ}$  once in 1929, six times in 1930, and eight times in 1931. On 21 December 1931 a sudden calm accompanied by sharp frost caused ice to form on the surface when the whole of the water was at a uniform temperature of  $4.0^{\circ}$ .

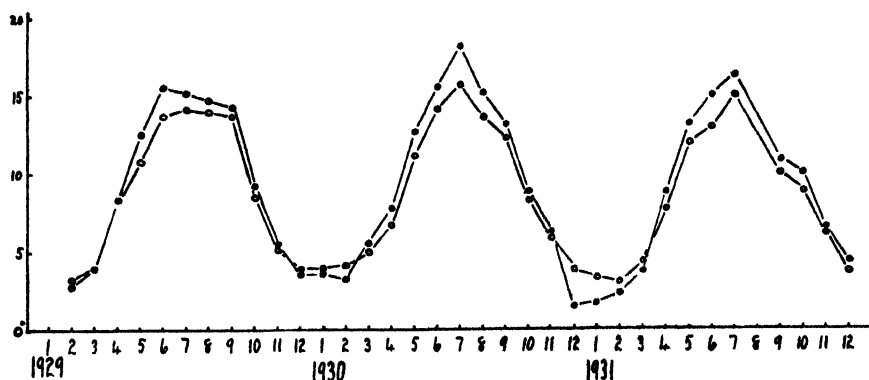


FIG. 3.—AVERAGE MONTHLY TEMPERATURES from February 1929 to December 1931.  
—●—, upper layer at T, fig. 2; —○—, lower layer at B, fig. 2.

A further factor in preventing stratification of the water is the occurrence of convection currents when the top layer of water cools at night and sinks down, reversing the temperature-gradient. No observations on the point were made at Butterby, but Beadle (4) and Worthington (25) show that the factor is important in shallow waters.

Temperature conditions in the pool may be summarized as follows:—

- (a) The temperature of the whole volume of water follows the atmospheric temperature fairly closely.
- (b) There is no separation into an epilimnion and a hypolimnion, and no seasonal alternation of stagnation and overturn. In summer and in winter there is a slight tendency to stratify, but windiness prevents actual stratification from taking place.
- (c) Owing to the action of the wind in winter, the temperature of the whole volume of water may fall below  $4.0^{\circ}$  to as low as  $2.0^{\circ}$ .



## THE OXYGEN CONTENT.

Each week, samples of water were obtained from the following points in the pool :—

- (a) From the top layer of water at 1 ft. 6 in. depth at point T, fig. 2, in the middle of the open water, M, fig. 1.
- (b) From the bottom layer of water at one foot from the floor of the pool at B, fig. 2, immediately below M, fig. 1.
- (c) From the top layer at a depth of 1 ft. 6 in. at S, fig. 1 and fig. 2, among the *Nuphar* leaves where the water was 3 ft. 6 in. deep.

The samples were obtained by clamping a displacement bottle of 270 c.c. capacity, to a pole, and swiftly thrusting the pole down to the required depth. The oxygen-content was determined by Winkler's method as given by Thresh and Beale (25). The determinations were carried out on the spot in the small laboratory on the west bank of the pool. A sample in triplicate, made at one spot in the pool on 21 April 1932, gave results of 8.64, 8.68, and 8.63 mg. per litre.

The weekly records of the oxygen-contents in mg. per litre of the top and bottom layers (T & B, fig. 2), and also the records for collecting-staion S, figs. 1 & 2, are given in Appendix 2. The weekly temperatures show a succession of variations, which is repeated more or less closely from year to year as far as the summer and autumn temperatures are concerned, but the winter and spring records show considerable differences from one year to another. The latter records for 1929, 1930, 1931 (and also for the 1933-4 season) are given in fig. 5, and will be discussed later.

The following table summarizes the variations in oxygen content noted throughout the whole period of observation :—

TABLE II.

Maximum and minimum O-contents.	Supersaturation.
Top :    max. 22.03, Feb. 1930. min. 1.7, Sept. 1929.	1930, Feb.-Mar., 5 times. 1931, Feb., once.
Bottom : max. 14.0, Feb. 1931. min. 0.0, Aug. 1930.	Below 1 mg. per litre. 1929, June-Sept., 3 times. 1930, June-Sept., 8 times.

The minimum oxygen records are probably too low, because no allowance was made for the presence of sulphides. On 18 June 1929 and 26 August 1930 the bottom samples of water had an odour of sulphuretted hydrogen, and it is probable, therefore, that the oxygen figures should read higher than those given by the Winkler test.

Fig. 4 shows the average monthly oxygen contents, calculated from the weekly observations, for the Top, Bottom, and Side (S, fig. 2), for the whole period of investigation. The record includes three preliminary collections made in February to March 1929. There is also shown the amounts of oxygen capable of being absorbed from the air to saturation point at the given temperature.

Comparison of the foregoing records shows that there is a fluctuation in the amount of oxygen from week to week, but that when the fluctuations are considered as a whole there is a steady rise and fall throughout the season. The oxygen-content of the top layer of water reaches its maximum in the middle of February and in early March, when supersaturation may take place. The supersaturation is associated with a maximum abundance of phytoplankton,

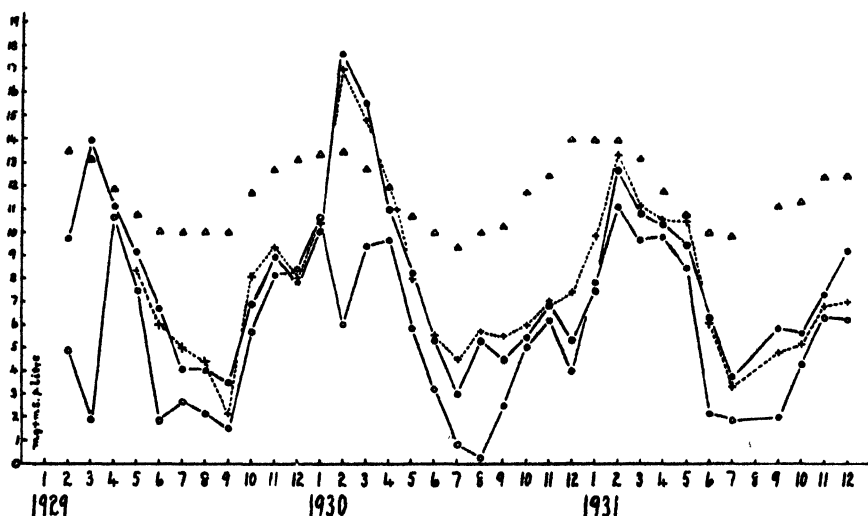


FIG. 4.—AVERAGE MONTHLY OXYGEN-CONTENTS from February 1929 to December 1931.  
—●—, at T, fig. 2; —○—, at B, fig. 2; —×—, at S, fig. 2; △, oxygen saturation.

consisting mainly of *Dinobryon*, *Uroglenopsis*, and *Eudorina*. The oxygen-content falls rapidly in May and June, keeps low from June onwards, and shows a minimum in August or September and not when the summer temperature is at its highest. The autumnal minimum may be due to the decay of the floating leaves of *Nuphar*, which sets in about this time and provides a large quantity of fermentable matter. After September the depletion of the oxygen is compensated by the autumnal fall in temperature, which increases the solubility of oxygen and brings in oxygen from the atmosphere. There is a second but smaller fall in December, which may be due to the final fermentation by the biota of the mud of the disintegrating fragments of *Nuphar* leaves which have sunk to the bottom.

The oxygen-content of the bottom layer of water is generally less than that of the top layer, except in winter, when the temperature of the water falls below 4° C. and an inverse temperature gradient occurs.

The oxygen-content of the top layer in the middle of the open water (M, fig. 1; T, fig. 2) differs from that among the *Nuphar* leaves (S, figs. 1 & 2), and is on the whole more often lower than the latter (see fig. 4). The difference is not due to the giving off of oxygen from the *Nuphar* leaves, because the difference is

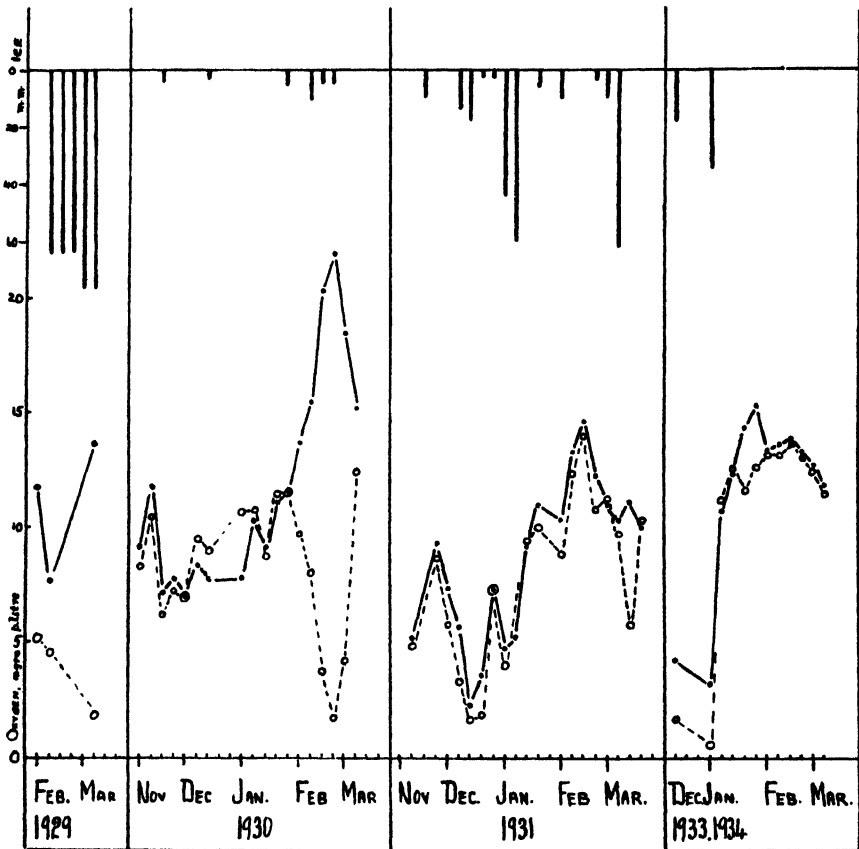


FIG. 5.—For explanation, see text.

maintained after the leaves have decayed and before the new leaves have appeared. The more probable reason is that the collecting station S is in shallower water nearer the margin of the pool, where diffusion of oxygen from the atmosphere is accelerated by ripple action and convection currents.

It has been mentioned previously that, whereas the summer and autumn variations in oxygen-content were fairly similar year by year, the winter and

spring records show marked differences. In fig. 5 are shown the weekly oxygen-contents in mg. per litre for the winter to spring periods of February to March 1929, November to March 1929-30, November to March 1930-1, and also December to March 1933-4. In addition, there is shown the thickness of ice when present at the time of collection. The oxygen-contents taken in February to March 1929 were preliminary to the regular collections and are not a complete series.

The two seasons 1929-30 and 1930-1 differ very markedly in the sequence of oxygen-contents. In the former there is an extraordinary supersaturation in the upper layer, accompanied by a great deficiency of oxygen in the lower layer, but in the latter period (and in 1933-4) the supersaturation is much less marked and there are only slight indications of deficiency in the lower layer, and for the most part the variations in the top and bottom oxygen-content are similar. The most obvious factor differentiating the seasons is the duration and thickness of the ice. In the 1929-30 season the ice was thin, and in the other season the ice was thick. The first effect of the presence of ice is to prevent wind-action, and consequently to keep the bottom layer of water in contact with the mud. The oxygen-content of the bottom layer tends to fall, especially if the ice-cover persists for several weeks. This effect is seen fairly consistently in fig. 5. When the ice melts, and wind-action can begin again, there is a quick rise in the oxygen-content of the bottom layer, and the change is accelerated by the warmer water at the surface (between 0° and 4°) becoming denser and sinking.

The situation is complicated, however, by the evolution of photosynthetic oxygen by the phytoplankton, which tends in this pool to be at its maximum about this time. If the ice is thin, light can penetrate freely, and as the ice-cover hinders or prevents the oxygen diffusing into the atmosphere, there may be a supersaturation in the upper layers, while at the same time there is a depletion of oxygen in the bottom layers. (See fig. 5; March 1929, February 1930, and possibly February 1931. March 1931 and January 1934 may perhaps be similar, because there may have been thin ice on the pool for some or all of the six days between the time of one weekly collection and the next.) If, on the other hand, the ice is not thin but thick, light penetration is hindered, and, instead of a supersaturation in the top layer, there is a general depression of the oxygen-content. (See fig. 5: February 1929, January 1931, March 1931, December to January 1934.) When the thick ice melts, light penetrates freely again, the oxygenated top layer sinks, wind-circulation is resumed, and the oxygen-content of both top and bottom layers increases. (See fig. 5: January 1931, March 1931, January 1934.)

A similar occurrence of supersaturation in the upper layer, combined with depletion in the bottom layer, during the ice-period, is recorded by Birge and Juday for Lake Mendota (see Thienemann, 22), and, as in the Long Pool, the thaw is followed by a general mixing of the layers and a more uniform distribution of the oxygen.

The variation in oxygen-content is due to two factors: firstly, the varying solubility of oxygen in water at different temperatures, and, secondly, the influence of the respiratory and photosynthetic activities of the biota of the pool. In fig. 4 the oxygen-saturation graph, calculated on average monthly temperatures from the oxygen-saturation data of Kaye and Laby (13), is superposed on the graphs of the observed oxygen-contents of the water. It is at once evident that the factor of physical solubility does not account for the observed variations in oxygen-content. Not only is the latter very much greater, but the inverse correlation with the temperature is only very partial and there may be a lag of a month, e.g. June 1929, August 1929, December 1929, July 1930, or a longer period, e.g. June to September 1929, December to February 1930-1, between the temperature maximum and the corresponding oxygen minimum. On eliminating the influence of varying oxygen-solubility by the device of expressing the oxygen-contents as percentages of saturation, a graph is obtained which very closely resembles that of the oxygen-content itself, as of course inspection of fig. 4 would lead us to expect. The oxygen percentage saturation graph is not shown in the text, but the percentage figures are given in Appendix 2. It is clear that in this pool the oxygen-content is determined very largely by a factor other than the solubility. The most probable factor is the respiratory activities of the biota of the mud which entirely covers the floor of the pool. The pool is small and shallow, and the ratio of the area of the bottom to the volume of water is high, so that the influence of the mud-biota tends to be very great. Added to this is the oxygen depletion caused by the decay of the leaves of the *Nuphar* society, which is also reflected in the graph. Miyadi (15) has shown experimentally that a eutrophic lake deposit completely de-oxygenated the water sample in less than eight hours, and Carter and Beadle (7) and Beadle (4) have shown the de-oxygenating power of the mud in Paraguayan and East African swamps. A further factor in the Long Pool, may be the great preponderance of zooplankton over phytoplankton. The zooplankton of rotifers and daphnids is more or less abundant throughout the year, and it is only in the colder months that the phytoplankton occurs in any quantity.

Oxygen-content conditions in the pool may be summarized as follows:—

- (a) The oxygen is fairly uniformly distributed throughout the water of the pool, and there is no differentiation into a well-oxygenated upper layer and a poorly-oxygenated lower layer, except occasionally in winter, when the surface is covered for some weeks with thin ice.
- (b) The oxygen-content varies from supersaturation (Top, 22.03 mg. per litre; Bottom, 14.0) in late winter and early spring, almost to complete absence (Top, 1.7; Bottom, 0.0) in late summer and autumn.
- (c) The amount of oxygen depends to a small extent on the photosynthetic oxygen of the phytoplankton, but mainly on the oxygen-depleting activities of the mud-biota, the macrophytes, and possibly the predominant zooplankton.

## THE PLANKTON.

During most of the year the major part of the plankton consists of Rotifers together with Daphnids and the larvae of the fly *Corethra plumicornis* (*Chaobrus crystallinus*), and during the summer the plankton consists almost wholly of these organisms. The phytoplankton is almost always small in amount, and consists mainly of *Synura*, *Dinobryon*, *Uroglenopsis*, and *Eudorina*. The phytoplankton is most abundant from early winter to spring, and in summer there is scarcely any. The plankton is most abundant in the littoral (at S, figs. 1 & 2), less abundant in the middle (at M, fig. 1; T, fig. 2), and least

TABLE III.

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
<b>PHYTOPLANKTONS.</b>																
<i>Peridinium Marssonii</i> . . . . .	x	x	x	x	x	x	x	..	..	..	..	x	x	x	x	x
<i>Peridinium aciculiferum</i> . . . . .	x	x	x	x	x	..	..	..	..	..	..	o	o	..	x	x
<i>Mallomonas acaroides</i> . . . . .	..	..	..	..	..	..	x	x	..	x	x	x	..	..	..	..
<i>Synura uvella</i> . . . . .	x	x	x	x	x	x	x	..	..	..	..	..	x	x	x	x
<i>Uroglenopsis americana</i> . . . . .	..	x	x	x	x	x	x	..	..	..	..	..	..	x	x	x
<i>Dinobryon sertularia</i> . . . . .	..	o	x	x	x	x	x	x	..	..	..	..	o	o	x	x
<i>Cryptomonas ovata</i> . . . . .	..	..	x	x	x	..	..	..	..	..	..	x	x	x	..	..
<i>Euglena</i> sp. . . . .	..	..	..	..	..	..	..	o	o	x	x	x	x	..	..	..
<i>Chlamydomonas nivalis</i> . . . . .	x	x	x	x	x	..	..	..	..	..	..	..	x	x	x	x
<i>Eudorina elegans</i> . . . . .	..	x	x	x	x	x	x	x	..	..	..	..	x	x	x	x
<i>Fragilaria capucina</i> . . . . .	..	..	..	x	x	x	x	..	..	x	x	x	..	..	..	..
<b>ZOOPLANKTONS.</b>																
<i>Anuraeopsis fissa</i> . . . . .	..	..	..	..	..	..	x	x	x	x	x	x	x	..	..	..
<i>Filinia longiseta</i> . . . . .	..	o	o	o	x	x	x	..	..	..	..	..	..	..	..	..
<i>Keratella quadrata</i> . . . . .	x	x	x	x	x	x	x	x	..	..	..	x	x	x	x	x
<i>Daphnia</i> . . . . .	x	x	..	..	..	x	x	x	x	x	x	x	x	x	..	..
Copepoda . . . . .	..	..	..	..	..	..	x	x	x	x	x	x	x	..	..	..
Decay of <i>Nuphar</i> leaves . . . . .	x	x	x	..	..	..	..	..	..	..	x	x	x	x	x	x
Period of inflow of water . . . . .	x	x	x	x	x	x	x	o	..	..	..	o	o	x	x	x

abundant near the bottom in the deep water (at B, fig. 2). On 12 May 1930, 15 litres of water from T yielded 0.6 c.c. of plankton, of which the dry weight was 0.0129 gm., or 860 mg. per cu. metre. The corresponding collection from B yielded only one-third that amount. The amount of dry net-plankton approximates to that found by Birge and Juday (6, p. 142, and Table 5, p. 186) in the smaller and shallower Wisconsin Lakes.

In addition to ascertaining the general periodicity of the principal planktons, observations were made of their origin and distribution. Three collecting

stations were selected, viz. :—(a) From the surface layer in the middle of the open water at M, fig. 1 (T, fig. 2) ; (b) From the surface layer near the side among the *Nuphar* plants at S, figs. 1 & 2 ; (c) From the layer one foot off the bottom in the middle of the pool at B, fig. 2. Some collections were also made at D, figs. 1 & 2. The collections were taken by means of the plankton-pump and collecting-jar described on p. 394, and were made at the times stated there.

The periodicities and distributions of some twelve phytoplanktons and nine zooplanktons were observed for three seasons. The general periodicities are given in Table III. In the Table, the sign  $\times$  indicates that the plankton occurred in that month during each season, and the sign o that it occurred in that month during some seasons but not in all three.

It was found that planktons varied (a) in the regularity of their periodicity from one season to another ; (b) in general continuity of occurrence during their seasonal period, i.e. they may be absent from all three collecting-stations for one or more weeks ; and (c) in continuity of occurrence in any one collecting-station. The reasons for these irregularities will be discussed in a later section (see p. 407).

## PHYTOPLANKTONS.

1. *PERIDINIUM MARSSONII* Lemm. (Lemmermann (14), p. 678 ; Schilling (18)). This Peridinium occurs in other small pools in the district (Griffiths and Cooke (11)). It has slightly concave plates bounded by upright wing-like bands. It began its period by an isolated occurrence on the bottom (B) in October 1929, after which it was not found in any station for six weeks. In the third week in November it occurred plentifully at S and less abundantly at M, but was not found at B. The continuity of its occurrence was broken in February and April, but at the end of the latter month it reached its maximum abundance and died out in the third week in May, a date corresponding to its disappearance in the previous 1929 season. In the 1930–1 season it again made its first appearance at B in October, but it was not found again until April 1931, after which it maintained continuity of occurrence until it finished its period in May. It was not found again in 1931. The organism seems fairly definitely to originate on the bottom and to spread to the middle and side. Its periodicity is irregular, and its occurrence tends to be discontinuous. It tends to be more plentiful at M and S than at B.

2. *PERIDINIUM ACICULIFERUM* Lemm. first appeared in the third week in November 1929 at M and S, but was not found again until the first week in January 1930, when it again occurred at M and S. After this its occurrence was continuous, mainly at M and S, but also at B. It reached its maximum abundance in March, and disappeared suddenly in the fourth week of that month. In the next season it appeared at M and S for the first two weeks of February,

and then disappeared until the fourth week in November 1931 when it appeared at S. It was not found subsequently. G. S. West (23) found that the alga had a periodicity from February to March in Bracebridge Pool, Warwickshire. Lemmermann (14) records it from February to April in the Muggelsee. In the Long Pool its periodicity is irregular, but its occurrence is fairly continuous. It seems to originate in the littoral rather on the bottom, and is never plentiful in the bottom collections.

3. *MALLOMONAS ACAROIDES* Perty is irregular in periodicity and in occurrence. It occurred at B in the second week in October 1929, and was not found again until the fourth week in May 1930, when it was found in all stations, though most abundantly at B. It again vanished until the first week in August, when it was found in abundance at M and S, where it continued until the end of November. In 1931 it appeared in abundance in all stations at the end of May and disappeared in June. It appeared again at B in October 1931, spread to M and S, and continued there until December, when the observations were concluded. It probably originates on the bottom, but during its occurrence it tends to be most plentiful at S and M.

4. *SYNURA UVELLA* Ehr. has a fairly regular periodicity, occurring from about November to May, and its occurrence is fairly continuous, but its distribution in the stations is irregular. In 1930 it was always least plentiful on the bottom, but in 1931 its distribution was more uniform.

5. *UROGLENOPSIS AMERICANA* (Calkins) Lemm. (Lemmermann (14), p. 449; Pascher (16)). This colonial Flagellate differs from *Uroglena volvox* Ehr. in having no dichotomously branched threads in the mucous investment, and in having a smooth cyst instead of a spinous one. It does not seem to have been recorded in this country until 1933, when Dr. W. H. Pearsall found it in Windermere (Pearsall, 17). In the Long Pool it has a fairly regular periodicity (see Table III), occurring from December or January to April or May. It attains its maximum about April, when cysts are formed in abundance. It appears to originate in the littoral and not on the bottom, and spreads from the littoral to the middle and bottom.

6. *CHLAMYDOMONAS NIVALIS* Wille (?). The alga has all the cell-characteristics of *C. nivalis*, but no resting stage was observed to confirm the diagnosis. It is an exclusively winter species, occurring from November 1928 to March 1929, January to March 1930, December 1930 to February 1931, and from November 1931 onwards. It originates at S and spreads to M, but it is seldom plentiful at B. Its periodicity is regular, and its occurrence is continuous.

7. *EUDORINA ELEGANS* Ehr. has a general periodicity from about December to May, but there were sporadic occurrences in the autumn of 1930 and 1931 also. It is usually more abundant at S at the beginning and end of its course, and is



more plentiful at S and M than at B. The egg-stage was very rare, and was observed in collections from S on 3 June 1930 and 19 May 1931.

8. *DINOBYON SERTULARIA* Ehr. occurred fairly regularly from January to June, but in 1931 it also occurred in August and September. Its origin is doubtful, but its tendency to avoid the bottom and to be most abundant in the littoral points to a littoral origin. In January 1930 it originated at M and B, but disappeared from M to appear at S in the following week. In February 1931 it originated at S.

9. *FRAGILARIA CAPUCINA* Desmaz. was one of the very few constant diatoms of the alga-flora. It has a double periodicity. There is a spring occurrence in February, April, or May, when the alga is mostly a littoral or bottom form, though in 1930 it also was found in the middle collection. The spring appearance is followed by a blank period until August or September, when the alga swarms around the decaying floating leaves of *Nuphar*, and floats out into the open water. It disappears in December. It undoubtedly originates at the bottom and side.

All the above phytoplanktonts were present in 1929, 1930, and 1931, and may, therefore, be considered as constant constituents of the phytoplankton. A number of phytoplanktonts, however, occurred less regularly, and a few were extraordinarily limited in the duration of their occurrence, although abundant at the time. They were as follows :—

10. *EUGLENA* sp. did not occur in 1929, but appeared in quantity at S and in lesser amount at M from August to November 1930 and from June to November 1931.

11. *CRYPTOMONAS OVATA* Ehr. was absent during 1929 and 1930, but appeared at B and spread to S from January to March 1931 and again in October to December.

12. *BOTRYOCOCCUS BRAUNII* Kutz. occurred in small numbers from October to November 1928 and on 2 January and 1 July 1930.

13. *DICTYOSPHAERIUM PULCHELLUM* Wood occurred in the littoral and bottom collections from 16 May to 19 June 1929 and again on 22 April 1930.

14. The following species of *Closterium* were found at S only :—*C. gracile* Breb., August and September 1930 ; *C. Venus* Kutz., September and October 1930 ; *C. acerosum* (Schrank) Ehr., October to November 1930 ; *C. rostratum* Ehr., November to December 1930 and also in February 1931. The numbers found were always very small.

The above phytoplanktonts were never plentiful during their periods of occurrence, but in the two following, although the periods were very short, the algae occurred in great abundance.

15. *ASTERIONELLA FORMOSA* Hass. appeared only once, namely, on 19 June 1929, when it was found in abundance at M and less abundantly at S. It had not been seen in the pool before ; it was found only in the one week, and it has not occurred since.

16. *SYNEDRA ACUS* Kutz. appeared in abundance for two weeks, 22 & 29 April 1930, and like *Asterionella* it has not occurred since.

### ZOOPLANKTONTS.

The bulk of the plankton of the pool consisted of Rotifers and Daphnids, together with the larvae of the Culicid fly, *Corethra plumicornis* (*Chaobrus crystallinus*). The Rotifers sometimes occurred in such abundance that the water was coloured by them. On the whole, both the periodicity and the distribution of the zooplanktonts were less irregular than in the phytoplanktonts.

1. *ANURAEOPSIS FISSA* (Gosse) Harring (Harring, 12, p. 13) ; *Anuraeopsis hypelasma* Gosse (Dieffenbach, 8). This Rotifer has a fairly regular periodicity from about May to November. Ahlstrom (I) records it from July to October in an Ohio pool. It tends to be more abundant at B and S than at M, but its distribution in the stations is variable.

2. *FILINIA LONGISETA* (Ehr.) Harring ; *Triarthra longiseta* Ehr. Its main period of occurrence is in spring and early summer, but there was also a winter phase in 1929-30. It is most plentiful at B and S, and tends to avoid the open water. Ahlstrom (I) records it as occurring from July to October.

3. *KERATELLA QUADRATA* (Muller) Harring ; *Anuraea aculeata* Ehr. Occurred in abundance almost all the year round, but was least abundant from July to September, and most abundant from March to May. There were two forms present, one with long posterior spines on the lorica and the other with shorter spines. The long-spined form was usually much more numerous in the open water at M than the short-spined form, but the latter was more numerous than the former on the bottom. Both forms were abundant in the littoral at S.

4. *POLYARTHRA TRIGLA* Ehr., *P. PLATYPTERA* Ehr., also occurred in great abundance most of the year.

5. *DAPHNIA PULEX* and *DAPHNIA LONGISPINA* occurred in great abundance in summer, often in extensive clouds or shoals. They occurred in the bottom collections in spring, and spread to the littoral and open water later. In December they went to the bottom again. Ehippia were observed on 2 December 1930 and 29 September 1931.

6. Copepoda were few and almost exclusively confined to the littoral, where they occurred from May to December.

7. Larva of *CORETHRA PLUMICORNIS* ; *CHAOBRUS CRYSTALLINUS* ; *Corethra* is not given in Wingate's list of Durham Diptera (Wingate, 24), and the larva does not occur in the adjacent Boathouse Pool or in any other of the many pools I have examined in the district. The fly emerges in April. The young larvae appear in May in the bottom and littoral collections, and later on they invade the open water. In October 1929 and 1930, when the temperature fell, the larvae suddenly went to the bottom and more or less remained there until the spring, but in 1931 this descent did not occur, though there was a tendency for the larvae to abandon the open water and move to the littoral.

As in the phytoplanktons, there were some zoo-planktons which appeared for a short time only, but no instance was observed of sporadic dominance comparable with that of *Asterionella* and *Synedra*. The following sporadics were noted, all of them being Rotifers :—

8. *TRICHOTRIA TETRACTIS* (Ehr.) Harring ; *Dinocharis tetractis* Ehr. Occurred at M and S in November and December 1929, November 1930, May 1931.

9. *PLATIAS QUADRICORNIS* (Ehr.) ; *Noteus quadricornis* Ehr. Occurred once only at B and S, July 1931.

10. *ROTARIA NEPTUNIA* (Ehr.) Harring ; *Rotifer neptunia* Ehr. Occurred once only in July 1931 at B.

11. *KERATELLA COCHLEARIS* (Gosse) Harring ; *Anuraea cochlearis* Gosse. Occurred once only in August 1931 at B.

The variability in the occurrence, periodicity, and distribution of the planktons is due to several causes :—

(a) *The turbulence of the water*.—The pool is small and shallow and is exposed to the sweep of every wind except from the south-east. The temperature records show that at all seasons there is a stirring and mixing of the whole volume of water. The turbulence of the water tends to cause a transference of any organism from its region of origin to other parts of the pool. The records of the collecting stations show that planktons sometimes are found to originate at one definite region, and sometimes are found in all parts of the pool when first observed. Planktons may apparently disappear from the collecting stations for a time and then re-appear again. In organisms which multiply rapidly, water movements tend to disperse them rapidly all over the pool, but if the multiplication is slow, the organisms may be carried away from the region in which they were first observed, and so disappear for a time.

It is noteworthy that almost all the planktonts are automotile organisms, and it is probable that the character of motility is of advantage in this habitat because it enables the organism to carry out photo-, chemo-, and aerotactic movements more readily, and thus to cope more readily with the possibility of being drifted away from more favourable into less favourable regions of the habitat. The records show that the planktonts tend to be more abundant in some situations than in others, e.g. in the well-lighted surface layers, or near the bottom, or in the open water, and automotility would seem to be a necessity if the organism is to maintain or regain its position in the appropriate habitat. A further characteristic of most of the planktonts is the production of resting-cysts or eggs, and this feature may again be a device for coping with the changing conditions of the habitat.

(b) *Fluctuation in water-level.*—Owing to the intermittent character of the water-supply (see next section), the pool varies considerably in level. There is an overflow period from about January to April, after which the level sinks steadily until September or October. The yearly falls from overflow level were as follows :—1929, 23 in., 22 October ; 1930, 9 in., 15 July ; 1931, 2 in., 28 October ; (1932, 12 in., 4 October ; 1933, 20 in., 19 September). The fall in level increases the ratio between the area of the bottom and the volume of water, and accentuates the effects of the biota of the mud upon the composition of the water. A further effect of the variation in water-level is that the adjacent *Typha* Marsh is put into communication with the pool during high water and is cut off during low. The occurrence of species of *Closterium* at collecting-station S may be due to the rising water flooding the Marsh. Fluctuations in level from year to year tend to modify the factor-complex of the habitat, and may possibly account for the complete, or partial absence of some planktonts in various years.

(c) *Intermittent water-supply.*—The water-supply of the pool is not a constant flow, but intermittent. During the summer and early autumn no water flows into the pool, the inflow ditches are dry, and the pool is in a state of complete isolation and self-subsistence as far as nutrient salts are concerned. The periods during which there was no inflow were as follows :—1929, May to December, twenty-nine weeks ; 1930, June to September, fourteen weeks ; 1931, July to November, fifteen weeks. The period varies from year to year, but in general is from June or July to October or November. There is a definite coincidence between the period of inflow and the period of the occurrence of the phytoplankton (see Table II, p. 402), namely, from late autumn to spring. *Peridinium aciculiferum* has a period of occurrence from November to March in the Long Pool, coincident with the period of inflow, but in the much larger Bracebridge Pool, Warwickshire (West, 23), and in the Muggelsee (Lemmermann, 14), its period is from February to March or April. *Eudorina* is a winter-period planktont in the Long Pool, but is a summer planktont in some of the

larger pools and meres of the lowlands (Griffiths, 9). The rotifer *Filinia longiseta* is here a winter form, but Ahlstrom (1) records it for July to October. Atkins and Harris (3) have shown that in certain small pools the inflow is the chief source of nutrient salts and affects the periodicity of the plankton. It would seem probable, therefore, that conditions are somewhat similar in the Long Pool.

(d) *The influence of the abundant macrophyta.*—Three-quarters of the area in which the collections were made is occupied by a community of *Nuphar luteum*. The submerged leaves appear under the water in April, and the floating leaves appear at the surface in May. The leaves begin to decay in August or September, and by November the floating leaves have disappeared and their disintegrating fragments have sunk to the bottom. Decay is continued on the bottom, and small brownish particles of decaying matter may be found suspended in the water as late as February. The decay is very complete, and the only traces left are the radiate sclerid cells of the petiolar lacunae, which may be found among the black amorphous particles of the bottom mud. It would seem probable that the growth of such a large volume of leaves must withdraw from the water a considerable amount of nutrient salts, and that when the leaves decay there will be a return of the material to the water. Reference to Table III, p. 402, shows clearly that the beginning of the occurrence of the phytoplankton coincides with the beginning of the decay of the *Nuphar* leaves, and that the termination of the phytoplankton coincides with the commencement of the new growth of *Nuphar*. Beadle (5) has shown in some East African lakes that the phosphate content of the water is affected by the growth and decay of aquatic macrophyta. Atkins (2) and Atkins and Harris (loc. cit.) show that phosphate is probably a limiting factor for plankton, and that the supply depends on inflowing water and the decay of organisms. It is probable, therefore, that the growth and decay of the *Nuphar* greatly modifies the amount of nutrient salts available for the phytoplankton, possibly more particularly in reference to phosphates.

(e) *The influence of the bottom mud.*—The floor of the pool is covered with a thick layer of black mud, consisting of autochthonous organic detritus, and thickly populated with a micro- and sub-micro fauna and flora. The activities of the biota of the mud include the withdrawal of oxygen from the water in which the planktons live, and diffusion into the water of carbon dioxide, sulphuretted hydrogen, and other gases, together with organic matter. In February 1934, when fermentation was presumably less active than in the warmer months of the year, the water contained 0.051/100,000 of free ammonia, 0.04 of albuminoid ammonia, and there was an oxygen-absorption figure of 0.32. In summer the presence of sulphuretted hydrogen is perceptible by its odour in the water samples. The effects of the metabolism of the mud-biota upon the composition of the water of the pool are probably the dominating feature of the economy

of the pool. These effects are accentuated by the variation in the volume of water from year to year, and may, therefore, be one of the causes of the variability in the occurrence, periodicity, and distribution of the plankton.

#### DISCUSSION.

The Long Pool belongs to the eutrophic type of lake, owing to the high salts-content, abundant sediments, and well-developed littoral vegetation, but it occupies an extreme position, and differs in several respects from the typical eutrophic lake as defined by Thienemann (21); see also Münster Ström (19, 20). The plankton of a typical eutrophic lake consists of Myxophyceae, Bacillarieae, and Peridinieae, of which *Anabaena*, *Aphanizomenon*, *Microcystis*, *Asterionella*, *Melosira*, and *Ceratium hirundinella* are representative types. The plankton of the Long Pool contains none of these, but consists of Chrysophyceae, e.g. *Mallomonas*, *Synura*, *Uroglenopsis*, *Dinobryon*, together with *Eudorina*, *Chlamydomonas*, *Euglaena*, *Peridinium aciculiferum* and *P. Marssonii*, and *Fragilaria capucina*. The two occurrences of *Asterionella* and *Synedra* were purely sporadic (see p. 406), and were probably casual introductions into the pool by the agency of the wild duck or swans which occasionally visit the Marsh.

There is also a striking difference in the periodicity of the plankton. In the typical eutrophic lake, as illustrated by Lake Mendota (Birge and Juday, 6), there is a spring maximum of Bacillarieae, a summer maximum of Myxophyceae, Chlorophyceae, and *Ceratium hirundinella*, an autumn maximum of Bacillarieae, and a winter minimum of plankton. In the Long Pool most of the phytoplanktonts occur only during the winter and early spring, and during the summer there is a plankton which consists almost wholly of rotifers and daphnids, together with larvae of *Corethra*.

There are also quantitative differences in the amount of dissolved solids and of dissolved gases such as sulphuretted hydrogen and ammonia. These differences are due to the absence of an epi- and hypolimnion, and the constant contact of the water with the very extensive littoral and bottom mud. The differences may be summed up as being due to the relative proportions of the lacustrine biotic communities in the respective eutrophic and Long Pool habitats. In the eutrophic habitat the three communities of (a) the littoral macrophyta, (b) the microbiota of the littoral and sub-littoral mud, and (c) the plankton, are such that the two former tend to be much less extensive than the last, because the area of weed-fringe and mud-fringe is small compared with the large area of open water in which the planktonts live. In the Long Pool the area of open water is less than a quarter of the area of the macrophytic zone, and the area of the mud zone is co-extensive with the floor of the basin of the pool. The volume of water at the disposal of the three communities is so small that the respective biota come into direct and close competition with one another, and the competition is accentuated by the non-replenishment of the volume of

water during periods when there is no inflow, and by the seasonal diminution of the volume from spring to late autumn. There is a marked inter-community competition superposed upon the normal inter-specific competition of each community, and it is this feature which most strongly differentiates the Long Pool from both the stratified and the unstratified type of eutrophic lake. In the latter, the area and volume of the water occupied by the plankton community is so large in relation to the other two communities that the eutrophic plankton is much less directly influenced by the other communities, even though it is not independent of them, and the expression of the competition, namely, the periodicity, is much less closely associated with the periodicity of the extra-planktonic communities than it is within the small and crowded habitat of the Long Pool.

The Long Pool represents a more or less extreme case of a kind of still-water which is very common in the lowland areas of this country. The characteristic feature of the type is the dominating influence of the benthos, and the type might well be differentiated by the name *benthic* and its plankton *benthoplankton*. There is, of course, every gradation to be found between the benthic type and the typical eutrophic still-waters, such as the meres of Shropshire, Cheshire, and Anglesey, and the Broadlands of Norfolk. These in turn grade into the semi-eutrophic Cumbrian lakes such as Windermere, and finally into the oligotrophic lakes such as Wastwater and those of Scotland and North Wales. In the oligotrophic habitat, the salts-content of the water, the inorganic and organic sediments, and the macrophyta are all in minimum amount, and the plankton is scanty and characterized by a desmid flora. In the eutrophic habitat, the three factors are at their optimum, and there is a high productivity of diatoms, blue-green algae, and *Ceratium*. In the 'benthic' habitat the three factors of salts, sediments, and macrophyta are beyond the optimum, and the phytoplankton becomes secondary to the zooplankton, and consists mainly of Chrysophyceae and a few of the lower Chlorophyceae.

I wish to express my very hearty thanks to Lt.-Col. H. C. J. Salvin of Croxdale Hall, Durham, for his permission to investigate Butterby Marsh, and to the Newcastle and Gateshead Water Company (Secretary and Manager, Mr. J. A. Coats) for a grant of £100 for laboratory, boat, and apparatus. I wish also to thank the following for information and assistance:—Mr. David Bryce, Dr. W. J. Fordham, Mr. J. T. Saunders, Mr. Omer-Cooper, and Dr. C. W. Gibby.

#### SUMMARY.

1. The Long Pool in Butterby Marsh, Durham, is 2.27 acres (0.91 hectares) in area, and has a maximum depth of 10 ft. (3 m.). Three-quarters of its area is occupied by *Nuphar luteum*, and it adjoins a marsh community of *Rumex*

*hydropathum* and *Typha latifolia*. Its floor consists of black autochthonous organic detritus. The water has a pH of 7.9-7.5, and contains 40 to 50/100,000 of dissolved solids.

2. The temperature of the whole volume of water follows the atmospheric temperature, and stratification is prevented by wind action.

3. The dissolved oxygen is fairly uniformly distributed throughout the whole volume of water, and varies in amount from supersaturation to almost complete depletion. There is no differentiation into a well-oxygenated upper and a poorly-oxygenated lower layer, except during prolonged periods of thin ice.

4. The plankton consists mainly of rotifers and daphnids, which are found throughout the year and most abundantly in summer. The phytoplankton consists of Chrysophyceae and lower Chlorophyceae and is even moderately abundant only during the colder months. The planktons tend to vary in their occurrence, distribution, and periodicity, and remarkable cases of sporadic abundance were noted.

5. The Long Pool is a benthic type of still-water in which the influence of the littoral and bottom biota is at its maximum, as contrasted with the optimum conditions in the eutrophic lake and with the minimum conditions in the oligotrophic lake.

## APPENDICES.

### APPENDIX 1.

#### TEMPERATURE °C.

#### UPPER LAYER, T.

#### LOWER LAYER, B.

Week.	1.	2.	3.	4.	5.	Av.	1.	2.	3.	4.	5.	Av.
1929.												
February ....	3.5	2.3	..	..	..	2.9	4.2	2.3	..	..	..	3.2
March .....	..	4.0	..	..	..	4.0	..	4.0	..	..	..	4.0
April .....	..	8.25	8.25	..	..	8.2	..	8.25	8.25	..	..	8.2
May .....	11.0	..	13.0	13.5	..	12.5	9.0	..	11.25	12.0	..	10.7
June .....	14.0	17.5	17.0	13.25	..	15.4	13.0	13.5	15.0	13.25	..	13.7
July .....	12.5	13.1	17.75	17.0	15.5	15.2	12.0	12.0	14.5	17.0	15.5	14.2
August .....	14.0	14.25	15.0	16.0	..	14.8	13.5	14.0	14.0	14.5	..	14.0
September ...	15.0	15.5	14.0	12.75	..	14.3	14.5	15.0	13.5	11.75	..	13.7
October .....	10.75	8.75	12.0	8.5	5.5	9.1	10.75	8.75	10.0	8.0	5.5	8.5
November ....	8.25	5.0	4.2	6.25	..	5.4	6.25	5.0	4.2	5.25	..	5.2
December ...	4.7	2.5	3.5	..	..	3.5	4.7	2.5	4.0	..	..	3.7



## APPENDIX 1 (cont.).

TEMPERATURE ° C.													
UPPER LAYER, T.							LOWER LAYER, B.						
Week.	1.	2.	3.	4.	5.	Av.	1.	2.	3.	4.	5.	Av.	
1930.													
January .....	3.5	5.5	2.5	3.5	3.0	3.6	3.5	5.5	2.75	3.75	3.5	3.8	
February .....	3.5	3.0	3.5	2.5	..	3.1	3.75	3.5	4.25	4.75	..	4.1	
March .....	6.0	6.0	4.0	6.0	..	5.5	5.0	5.5	4.0	5.5	..	5.0	
April .....	5.5	7.0	9.0	7.5	9.75	7.7	4.0	4.5	8.75	6.25	9.5	6.6	
May .....	11.0	10.0	13.0	16.5	..	12.6	10.5	9.0	11.75	13.0	..	11.1	
June .....	14.0	15.5	17.1	..	..	15.5	13.0	14.5	15.0	..	..	14.1	
July .....	20.75	17.5	16.0	..	..	18.1	15.75	16.0	15.0	..	..	15.6	
August .....	..	15.5	14.0	16.0	..	15.1	..	13.5	13.5	14.0	..	13.6	
September .....	15.0	13.5	12.5	13.0	11.5	13.1	14.0	13.0	12.0	11.5	11.0	12.3	
October .....	10.0	9.5	8.75	6.5	..	8.7	9.75	9.0	8.5	6.0	..	8.31	
November .....	6.5	6.75	..	5.0	..	6.1	6.5	6.75	..	4.5	..	5.9	
December .....	3.5	1.0	0.5	0.75	1.5	1.4	4.0	4.0	3.5	4.1	4.0	3.9	
1931.													
January .....	0.0	1.0	4.0	1.5	..	1.6	3.25	..	3.5	3.0	..	3.2	
February .....	0.0	4.0	2.0	3.0	..	2.2	2.5	4.0	2.0	3.5	..	3.0	
March .....	3.0	0.0	5.0	5.75	5.0	3.7	3.5	3.25	4.5	5.75	5.0	4.4	
April .....	9.0	10.0	6.5	9.75	..	8.8	7.25	9.0	6.0	8.5	..	7.7	
May .....	11.0	14.5	12.5	14.5	..	13.1	10.75	12.5	12.5	12.0	..	11.9	
June .....	13.5	15.0	15.5	15.0	16.0	15.0	13.0	11.5	12.5	13.5	14.5	13.0	
July .....	17.5	16.25	15.0	..	..	..	15.5	15.0	14.5	..	..	15.0	
August .....	..	..	..	..	..	..	..	..	..	..	..	..	
September .....	..	..	..	10.5	11.0	10.7	..	..	..	9.75	10.25	10.0	
October .....	14.5	11.75	8.25	5.5	..	10.0	11.3	11.0	8.5	5.0	..	8.9	
November .....	8.0	7.25	5.75	5.0	..	6.5	7.5	7.0	5.25	4.5	..	6.1	
December .....	4.75	4.0	4.5	..	..	4.4	4.25	3.0	4.0	..	..	3.7	

## APPENDIX 2.

OXYGEN, mg. per litre, weekly. Middle Region, M., fig. 1, T &amp; B, fig. 2.

UPPER LAYER, T.								LOWER LAYER, B.							
Week.	1.	2.	3.	4.	5.	Av.	% sat.	1.	2.	3.	4.	5.	Av.	% sat.	
1929.															
Feb. ....	11.82	7.67	..	..	..	9.74	72.1	5.17	4.51	..	..	..	4.84	36.2	
Mar. ...	..	13.86	..	..	..	13.86	106.0	..	1.84	..	..	..	1.84	14.1	

## APPENDIX 2 (cont.).

OXYGEN, mg. per litre, weekly. Middle Region, M., fig. 1, T &amp; B, fig 2.

UPPER LAYER, T.								LOWER LAYER, B.							
Week.	1.	2.	3.	4.	5.	Av.	% sat.	1.	2.	3.	4.	5.	Av.	% sat.	
1929.															
Apr. . . .	..	11.71	10.52	..	..	11.11	94.2	..	10.82	10.41	..	..	10.61	90.0	
May . . . .	11.0	..	9.63	6.95	..	9.19	86.3	11.59	..	6.84	4.10	..	7.51	69.8	
June . . . .	7.8	9.03	4.54	5.11	..	6.62	66.6	2.91	1.54	0.41	2.10	..	1.74	16.8	
July . . . .	3.45	4.99	3.15	..	4.7	4.07	40.3	3.09	3.50	2.24	..	1.7	2.63	25.4	
Aug. . . .	2.66	5.98	4.06	3.76	..	4.11	41.0	2.61	3.33	1.39	1.24	..	2.14	20.9	
Sept. . . .	5.98	1.70	2.29	4.33	..	3.57	35.2	2.29	0.47	1.95	1.41	..	1.53	14.7	
Oct. . . .	4.02	9.10	8.06	5.06	7.27	6.70	58.7	3.14	8.54	5.39	3.84	7.02	5.58	49.6	
Nov. . . .	9.20	11.79	7.20	7.74	..	8.98	71.4	8.48	10.58	6.37	7.33	..	8.19	64.6	
Dec. . . .	7.02	8.41	7.74	..	..	7.72	58.7	6.91	9.49	8.95	..	..	8.45	64.3	
1930.															
Jan. . . .	7.85	10.35	9.13	11.19	11.67	10.04	75.8	10.69	10.75	8.81	11.47	11.59	10.62	80.7	
Feb. . . .	13.74	15.48	20.55	22.03	..	17.95	133.6	9.67	7.99	3.78	2.80	..	6.06	46.3	
Mar. . . .	18.51	15.31	14.1	14.28	..	15.55	103.3	4.12	12.5	10.09	11.23	..	9.48	74.5	
Apr. . . .	9.97	11.61	11.79	10.21	11.06	10.93	91.6	7.93	10.45	11.05	9.85	9.07	9.67	78.7	
May . . . .	8.39	7.86	9.66	7.02	..	8.23	77.4	4.02	6.12	6.90	6.18	..	5.80	52.7	
June . . . .	5.94	5.62	4.37	..	..	5.31	53.4	4.74	4.09	0.72	..	..	3.18	31.3	
July . . . .	3.48	3.42	2.24	..	..	3.05	32.6	0.78	0.90	0.52	..	..	0.73	7.3	
Aug. . . .	..	4.39	5.94	5.55	..	5.29	52.8	..	0.21	0.36	0.0	..	0.19	1.8	
Sept. . . .	1.14	2.19	6.38	8.16	4.89	4.55	43.3	0.16	1.35	3.94	3.31	3.92	2.53	23.7	
Oct. . . .	3.9	7.32	5.15	6.16	..	5.63	48.3	3.36	6.06	5.48	5.60	..	5.12	43.5	
Nov. . . .	5.76	5.25	..	9.33	..	6.78	54.5	5.05	4.98	..	8.62	..	6.21	49.8	
Dec. . . .	7.44	5.61	2.38	3.52	7.31	5.25	37.5	5.88	3.41	1.61	1.79	7.4	4.02	30.7	
1931.															
Jan. . . .	4.74	5.34	9.12	11.07	..	7.57	54.3	4.08	..	9.35	10.08	..	7.83	58.6	
Feb. . . .	10.36	13.28	14.63	12.34	..	12.65	92.5	8.87	12.48	14.0	10.86	..	11.53	85.8	
Mar. . . .	11.12	10.40	11.17	10.0	11.37	10.81	82.2	11.38	9.75	5.77	10.44	11.09	9.68	74.8	
Apr. . . .	9.37	8.96	11.47	11.94	..	10.43	89.5	7.70	9.18	12.21	10.25	..	9.83	82.3	
May . . . .	11.83	11.22	8.32	6.83	..	9.55	92.5	11.03	9.74	8.06	5.40	..	8.55	79.6	
June . . . .	4.09	6.32	8.50	7.67	4.81	6.28	62.7	2.73	3.99	1.89	1.99	1.29	2.14	20.6	
July . . . .	3.47	4.07	3.58	..	..	3.71	38.1	1.02	1.67	2.76	..	..	1.82	18.2	
Aug. . . .	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Sept. . . .	..	..	..	6.74	4.82	5.78	52.2	..	..	..	2.80	1.40	2.10	18.6	
Oct. . . .	6.10	3.97	4.25	8.34	..	5.66	50.1	2.48	2.64	4.32	7.77	..	4.30	37.3	
Nov. . . .	10.19	6.10	3.86	9.29	..	7.36	60.1	9.67	3.94	3.13	8.64	..	6.34	51.7	
Dec. . . .	8.85	10.70	8.18	..	..	9.24	74.6	7.02	4.40	7.24	..	..	6.22	47.5	

## APPENDIX 2 (cont.).

OXYGEN, mg. per litre. weekly. Littoral Region, S, fig. 1.

Oxygen, mg. per litre, weekly. Littoral Region, S. fig. 1.																			
Week.	1.	2.	3	4.	5.	Av.	% sat.	Week.	1.	2.	3.	4.	5.	Av.	% sat.				
1929.								1930.											
May .....	8.50	..	8.80	7.61	..	8.30	77.8	September .	2.28	3.05	5.95	10.80	4.14	5.24	49.8				
June .....	6.70	7.53	5.17	4.73	..	6.03	60.7	October ...	4.33	7.92	5.46	6.48	..	6.05	51.9				
July .....	5.21	6.95	4.91	..	..	5.02	49.8	November..	5.64	5.46	..	9.12	..	6.74	54.1				
August ....	4.15	4.38	4.01	5.05	..	4.40	44.0	December .	7.68	..	..	..	7.18	7.43	53.1				
September .	2.24	1.59	2.58	..	..	2.14	21.1												
October ....	4.69	8.47	13.07	5.82	8.50	8.11	69.6	1931.											
November ...	9.39	11.27	8.89	7.87	..	9.35	74.3	January ...	..	..	9.78	..	..	9.78	70.1				
December .	6.28	9.57	..	..	..	7.92	60.2	February ..	11.94	..	14.58	..	..	13.26	96.2				
								March .....			11.16	9.91	12.36	11.14	84.6				
								April .....	9.52	8.71	13.14	10.10	..	10.37	88.9				
January ....	10.05	10.53	10.39	11.18	..	10.53	79.5	May .....	13.50	13.10	8.58	6.81	..	10.49	99.8				
February ....	9.57	..	19.26	22.12	..	16.98	126.3	June .....	4.78	6.24	9.26	4.89	3.4	5.71	57.0				
March .....	20.18	13.96	11.01	13.9	..	14.76	117.2	July .....	3.79	1.94	4.36	..	..	3.36	34.5				
April .....	10.47	11.52	11.49	10.53	11.37	11.07	92.6	August .....	..	..	..	..	..	..	..				
May .....	8.54	8.58	9.72	7.44	..	8.57	80.5	September .	..	..	..	5.77	3.79	4.78	43.1				
June .....	6.48	6.36	3.62	..	..	5.49	55.2	October ...	6.08	3.48	3.79	7.59	..	5.23	46.3				
July .....	3.74	6.89	2.86	..	..	4.49	47.9	November..	10.82	5.51	3.17	8.0	..	6.87	56.0				
August ....	..	3.78	5.76	7.32	..	5.62	56.1	December .	7.28	8.89	4.63	..	..	6.93	55.8				

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A contribution to our knowledge of the aquatic Phycomycetes of Great Britain. By F. K. SPARROW, Jr., Ph.D. (Communicated by F. T. BROOKS, M.A., F.R.S., F.L.S.)

(PLATES 14-20 and 7 Text-figures)

[Read 19 March 1936]

#### INTRODUCTION.

While the attention of mycologists has been directed for many years to a study of the fungous flora of the land, relatively little attention has been accorded to the myriad of microscopic forms to be found in abundance in fresh-water habitats. In Great Britain, some of the earliest accounts not only of the more ubiquitous Saprolegniaceous fungi but also of certain little-known Chytridiaceous forms were referred to by Berkeley in his interesting article 'Egg Parasites and their Relatives' ('The Intellectual Observer', 1864). Since then, information has not been accumulated at a rate commensurate with the undoubted importance of these organisms in the disintegration of organic complexes in nature, nor has there been a widespread appreciation of the features of more general biological interest which these forms often so strikingly reveal.

The object of the present investigation was to learn something of the aquatic fungous flora of a favourable locality in Great Britain, particularly to determine whether or not it was in reality so devoid of representatives of certain of the more primitive groups (Chytridiales, Blastocladales, Monoblepharidales) as records from the literature might indicate. Since work on this problem was initiated (July 1932), several papers have appeared by British mycologists (Barnes and Melville (1932)), Cook (1932), Cook and Forbes (1932), Forbes (1935)), which have considerably extended our knowledge of this flora. To the excellent researches of these authors the writer would include his own, which, it will be seen, does not entirely duplicate their findings, since, in addition to certain members of groups investigated by them, over one-half (39) of the sixty-seven fungi discussed herein belong to the Chytridiales—only a relatively few aquatic representatives of which have thus far been reported from the country.

It will readily be observed from Table I. that many more members of the Chytridiales, Blastocladales and Monoblepharidales were found than of certain other orders, notably the Saprolegniales and Ancylistales. This was not due in the first instance to the paucity of members of the Saprolegniales,

## OCCURRENCE.

TABLE I.—*Summary of species collected, substratum, locality and date of field collection.*

Species.	Substratum.	Locality.	Date.
<b>CHYTRIDIALES*.</b>			
? <i>Pseudolpidium Pythii</i> . . . . .	<i>Pythium</i> sp.	Mildenhall, Suffolk.	15. 10. 32.
<i>P. fusiforme</i> . . . . .	<i>Achlya</i> sp.	Coe Fen, Cambridge.	29. 11. 32.
<i>Woronina polycystis</i> . . . . .	<i>Achlya</i> spp.	Barton Mills, Suffolk.	14. 11. 32.
	"	Cambridge.	24. 12. 32.
	"	"	Jan.—May 1933.
? ( <i>Rozella</i> ) <i>septigena</i> . . . . .	<i>Saprolegnia</i> sp.	Barton Mills, Suffolk.	14. 11. 32.
	<i>Achlya</i> sp.	" " "	"
<i>Pleolpidium</i> ( <i>Rozella</i> ) <i>Polyphagi</i> Sparrow	<i>Polyphagus euglenae</i> . . . . .	Leys School, Cambs.	3. 3. 33.
<i>Olpidium gregarium</i> . . . . .	Rotifer eggs.	Site 4.	4. 3. 33.
<i>O. entophytum</i> . . . . .	<i>Cladophora</i> sp.	Cambridge.	8. 8. 32.
<i>O. endogenum</i> (?) . . . . .	<i>Mougeotia</i> sp.	Site 1.	20. 12. 32.
	<i>Zygnema</i> sp.	"	3. 3. 33.
? <i>Pleotrachelus Petersenii</i> . . . . .	"	"	"
<i>Septolpidium lineare</i> Sparrow	<i>Synedra</i> sp.	"	3. 9. 32.
<i>Chytridium olla</i> . . . . .	<i>Nitella tenuisima</i> (?).	Wicken Fen, Cambs.	29. 10. 32.
<i>C. Schenkii</i> . . . . .	<i>Oedogonium</i> sp.	Site 5.	20. 9. 32.
<i>Chytridium</i> sp. (gen. nov. ?).	<i>Aesculus</i> twigs.	Site 2.	10. 8. 32.
	<i>Quercus</i> twigs.	Kew Gardens.	1. 11. 32.
<i>C. lagenaria</i> . . . . .	<i>Rhizoclonium hieroglyphicum</i> .	Coe Fen, Cambridge.	29. 11. 32.
<i>C. versatile</i> . . . . .	<i>Synedra</i> sp.	Cambridge.	8. 8. 32.
	"	"	2. 11. 32.
<i>C. inflatum</i> . . . . .	<i>Oedogonium</i> sp.	Site 5.	20. 9. 32.
<i>C. appressum</i> . . . . .	<i>Melosira varians</i> .	Site 1.	18. 9. 32.
<i>C. sphaerocarpum</i> . . . . .	<i>Mougeotia</i> sp.	Coe Fen, Cambridge.	6. 9. 32.
	<i>Achlya</i> sp.	Barton Mills, Suffolk.	6. 11. 32.
	<i>Spirogyra</i> sp.	Site 1.	6. 3. 33.
<i>C. chaetophilum</i> . . . . .	<i>Bulbochaete</i> sp.	Wicken Fen, Cambs.	1. 8. 32.
	<i>Typha</i> pollen.	Site 5.	20. 9. 32.
<i>Rhizopidium subangulosum</i> (?).	<i>Oscillatoria</i> sp.	Leys School, Cambs.	13. 2. 33.
<i>R. lagenula</i> . . . . .	<i>Melosira varians</i> .	Site 1.	5. 9. 32.
	" "	Site 5.	20. 9. 32.
	" "	Coe Fen, Cambridge.	13. 2. 33.
<i>R. simplex</i> . . . . .	<i>Spirogyra</i> sp.	Site 1.	18. 9. 32.
	? <i>Chlorococcum</i> .	Site 5.	3. 3. 33.

\* To this list may be added the following species, collected in ridge integuments in the Cam at Cambridge in August 1935:—*Rhizidium mycoophilum*, *Rhizoclostratium globosum*.

TABLE I (cont.).

Species.	Substratum.	Locality.	Date.
<b>CHYTRIDIALES (cont.).</b>			
<i>Rhizophidium goniosporum</i> .	<i>Tribonema bombycina</i> var. <i>minor</i> .	Site 1.	6. 3. 33.
	<i>Tribonema bombycina</i> var. <i>minor</i> .	Site 4.	3. 3. 33.
<i>R. globosum</i> . . . . .	Rotifer.	Site 2.	8. 8. 32.
	<i>Typha</i> pollen.	"	"
	<i>Oscillatoria</i> sp.	Site 1.	18. 9. 32.
<i>R. carpophilum</i> . . . . .	<i>Achlya</i> spp.	Site 2.	21. 8. 32.
	<i>Monoblepharis macrandra</i> .	"	"
	<i>Dictyuchus monosporus</i> .	Kew Gardens.	1. 2. 33.
<i>R. sphaerocarpum</i> . . . . .	Nematode.	Site 4.	3. 3. 33.
<i>Phlyctochytrium</i> (?) <i>biporo-</i> <i>sum</i> .	<i>Spirogyra</i> sp.	Site 1.	18. 9. 32.
<i>P. quadricorne</i> . . . . .	<i>Cladophora</i> sp.	Cambridge.	8. 8. 32.
<i>P. laterale</i> , sp. n. . . . .	<i>Spirogyra</i> sp.	Site 1.	24. 5. 33.
<i>Scherffeliomyces parasitans</i> , nom. nov.	<i>Euglena</i> sp.	Site 4.	3. 3. 33.
<i>Podochytrium clavatum</i> . . . .	<i>Fragellaria</i> sp.	Site 5.	20. 9. 32.
<i>P. lanceolatum</i> Sparrow . . . .	<i>Melosira varians</i> .	Site 1.	26. 12. 32.
<i>Rhizidiopsis emmanuelensis</i> Sparrow . . . . .	" "	"	7. 3. 33.
<i>Entophlyctis apiculata</i> . . . .	(?) <i>Nitzschia</i> sp.	.....	....
<i>E. Cienkowskiana</i> . . . . .	<i>Euglena</i> sp.	Site 4.	3. 3. 33.
	<i>Spirogyra</i> sp.	Wicken Fen, Cambs.	1. 8. 32.
	"	Streighton, Cambs.	"
	<i>Cladophora</i> sp.	Cambridge.	3. 8. 32.
	<i>Vaucheria</i> sp.	Streighton, Cambs.	18. 9. 32.
	<i>Oedogonium</i> sp.	Site 5.	20. 9. 32.
<i>Cladochytrium replicatum</i> . . .	<i>Elodea</i> .	Site 2.	6. 8. 32.
	"	Wicken Fen.	9. 9. 32.
	Grass.	Cambridge.	11. 10. 32.
	"	Site 5.	20. 9. 32.
	"	Kew Gardens.	1. 11. 32.
<i>Nowakowskiella elegans</i> . . . .	<i>Elodea</i> .	Wicken Fen, Cambs.	9. 9. 32.
	"	Site 2.	2. 10. 32.
	Grass.	Cambridge.	11. 10. 32.
<i>Polyphagus Euglenae</i> . . . . .	<i>Euglena</i> sp.	Leys School, Cambs.	7. 2. 33.
	"	Site 4.	3. 3. 33.
? <i>Rhizidium</i> spp. . . . .	Vegetable debris.	Site 5.	20. 9. 32.
<b>BLASTOCLADIALES.</b>			
<i>Blastocladia ramosa</i> . . . . .	Apple fruit.	Site 3.	29. 11. 32.
<i>B. rostrata</i> . . . . .	<i>Aesoulus</i> twigs.	"	9. 9. 32.
<i>B. Pringsheimii</i> . . . . .	Twigs, apples.	Sites 1, 2, 3.	Whole year.

TABLE I (cont.).

Species.	Substratum.	Locality.	Date.
<b>BLASTOCLADIALES.</b>			
<i>Blastocladia glomerata</i> , sp. n.	<i>Aesculus</i> twigs.	Site 2.	24. 12. 32.
	" "	"	20. 4. 33.
<i>B. globosa</i> .....	Apple fruit.	Site 3.	Sept.-Dec. 1932.
<i>B. prolifera</i> .....	<i>Frazinus</i> twigs.	Coe Fen, Cambridge.	11. 10. 32.
<b>MONOBLEPHARIDALES.</b>			
<i>Gonapodya prolifera</i> .....	<i>Aesculus</i> twigs.	Site 2.	Aug.-Dec. 1932.
	<i>Quercus</i> twigs.	Site 5.	20. 9. 32.
	" "	Kew Gardens.	1. 11. 32.
<i>G. polymorpha</i> .....	" "	" "	"
<i>Monoblepharis macrandra</i> ..	<i>Aesculus</i> twigs.	Site 2.	Aug.-Dec. 1932.
	<i>Frazinus</i> twigs.	Barton Mills, Suffolk.	14. 11. 32.
<i>M. macrandra</i> var. <i>laevis</i> ..	<i>Aesculus</i> twigs.	Site 2.	24. 12. 32.
<i>M. ephaerica</i> .....	<i>Aesculus</i> (?) twigs.	"	"
<i>M. ovigera</i> .....	Hemp seed (bait).	Site 5.	20. 9. 32.
	Apple fruit.	Cambridge.	30. 11. 32.
	Twig.	Kew Gardens.	1. 2. 33.
<b>LEPTOMITALES.</b>			
<i>Rhipidium europaeum</i> .....	Apple fruit.	Site 3.	Throughout year.
	<i>Frazinus</i> twigs.	"	" "
	Twigs.	Site 2.	" "
<i>R. americanum</i> .....	<i>Quercus</i> twig.	Site 5.	20. 9. 32.
<i>Sapromyces Reinechii</i> .....	" "	"	"
<b>SAPROLEGNIALES.</b>			
<i>Saprolegnia asterophora</i> ....	Hemp seed (bait).	Mildenhall, Suffolk.	16. 11. 32.
<i>Achlya colorata</i> .....	Grass stem.	Site 5.	20. 9. 32.
<i>Dictyuchus monosporus</i> ....	Twigs, hemp seed.	Cambridge.	Throughout year.
	Twig.	Kew Gardens.	1. 11. 32.
	<i>Frazinus</i> twigs.	Barton Mills, Suffolk.	16. 11. 32.
<i>Thraustotheca clavata</i> .....	Hemp seed (bait).	York.	8. 9. 32.
<i>Aphanomycopeis bacillaria-</i> <i>cearum</i> .	<i>Synedra</i> sp.	Site 1.	8. 3. 33.
<i>Ectrogella monostoma</i> .....	"	"	"
<i>Aphanomyces parasiticus</i> ...	<i>Dictyuchus</i> .	Barton Mills, Suffolk.	16. 11. 32.
<b>ANCYLISTALES.</b>			
<i>Myzocyttium zoophthorum</i> , sp. n.	Rotifers.	Site 4.	3. 3. 33.



TABLE I (cont.).

Species.	Substratum.	Locality.	Date.
<b>PYTHIALES.</b>			
<i>Pythium tenue</i> .....	<i>Vaucheria</i> sp.	Streighton, Cambs.	18. 9. 32.
	"	Site 1.	12. 9. 32.
<i>P. perigynorum</i> , sp. n. ....	Hemp seed (bait).	Site 5.	20. 9. 32.
<i>Zoophagus insidians</i> .....	Rotifers.	Site 2.	9. 8. 32.
	"	Streighton, Cambs.	18. 9. 32.
	"	Coe Fen, Cambs.	26. 11. 32.
	"	Kew Gardens.	1. 2. 33.
<i>Pythiomorpha gonapodyides</i> ..	Twigs.	Cambridge.	Throughout year.
<i>Pythiogelon</i> spp. ....	"	"	" "
	Apple fruits.	"	" "
	<i>Frazinus</i> twigs.	Barton Mills, Suffolk.	14. 11. 32.
	" "	Site 5.	20. 9. 32.

but rather to the investigator's greater interest in the supposedly rare and lesser known fungi belonging to the first three groups. Since more data had been accumulated in the past concerning the Saprolegniales than any other of the truly aquatic orders, and as a study of these forms was already in progress in at least one other laboratory, it seemed better to concentrate on the remaining groups. With regard to the Ancylistales, it has been my experience that these fungi are, in fact, of very infrequent occurrence.

While the afore-mentioned table contains dates of collection, in most instances these are of little significance as indices of favourable times for collection. Thus, for *Gonapodya prolifera*, it was perhaps needless, save for a matter of record, to indicate any date, since this fungus, and perhaps to an even greater degree such forms as *Blastocladia Pringsheimii*, *Rhipidium* spp., etc., could be collected at all times and in any quantity, depending entirely on the presence and amount of the proper substratum (generally placed there by the investigator). The mild nature of the English winter makes it possible at all times, with the application of the proper technique, to have readily available at least a fair number of aquatic fungi.

For the purposes of the present study it seemed desirable to select a locality rich in readily accessible aquatic habitats, and in Cambridge this was ideally realized. Not only were there numerous favourable sites, but these were usually plentifully supplied with appropriate substrata—and, it might be remarked, even the tap-water yielded a rare fungus.

The majority of the organisms were collected in Cambridge or in the immediate vicinity. A smaller number were also obtained from debris collected in the pond to the rear of the Educational Museum, Haslemere,

Surrey (termed Site 5 in this paper), during the autumn foray of the British Mycological Society in 1932, and a few were found in the ponds in Kew Gardens. The localities of certain other collections are noted in the table.

Of the various sites in Cambridge, certain ones, because of the number of different forms they yielded, were outstanding. The small stream in Chapman's Garden, Emmanuel College (Site 1), which is fed by Hobson's Conduit, was especially notable for the variety of fungi which it contained, no fewer than seventeen, including two new genera and four new species, being collected there. Of the various ditches in or near the Colleges, that to the rear of Jesus College bordering on Midsummer Common (termed Site 2) yielded an abundance of twig-inhabiting forms such as species of *Monoblepharis*, *Blastocladia* and *Pythiogeton*, while the ditch in the rear of Peterhouse bordering Coe Fen (Site 3) furnished many fruit-inhabiting fungi such as *Rhipidium* and *Blastocladia*. It must not be supposed, however, that Site 2 was deficient in fruit-inhabiting forms, or that the Peterhouse ditch was lacking in xylophilous fungi, for these apparent differences were due at least in Peterhouse ditch to the difficulty of getting twigs because of the depth of the water, while the inquisitive nature of small boys made impractical the placing of traps containing fruits in Site 2. Several interesting fungi were obtained from a ditch on the Newnham-Granchester road by Trinity College playing field (termed Site 4). It is most probable that, provided the proper substratum is present, any of the numerous localities in Cambridge would yield a wide variety of Phycomycetous organisms.

#### METHODS OF COLLECTION.

As I have pointed out on previous occasions, the supposed rarity of many of these fungi seems due largely to a lack of knowledge of the methods of collection. Since the forms considered herein often possess morphological or developmental features of interest to mycologists and botanists in general, it might seem of value to interpolate practical hints on their collection:—

1. *Chytridiales*.—For the purposes of collection the fungi belonging to this group may be divided into parasites of (a) algae, (b) other aquatic fungi, (c) microscopic animals, (d) flowering plants. The last are not within the scope of this paper. In addition to these parasitic forms there are a large number which live on dead organic matter of both plant and animal origin.

(a) *Parasites of algae*.—While these may be occasionally found on material examined directly after collection, it has been my experience that a great number are found after the algae have been left in shallow dishes for a few days in the laboratory. In order to prevent excessive bacterial and protozoal development, care should be taken not to overcrowd the dish, since cultures once fouled by these organisms are useless. Species of *Spirogyra*, *Cladophora*,

*Tribonema*, and *Rhizoclonium* are particularly susceptible to attack by Chytridiaceous fungi. Dishes containing the algae should have in them just enough water to cover the plants. As development of the parasites occurs rapidly and is soon completed, the material should be closely watched and frequent samples taken, beginning twelve hours after collection. Other algae will generally appear in such cultures, on which fungi are often found. Great care should be taken to make frequent examinations of the scum formed around the edge of culture dishes. Both living and dead material of *Nitella* and *Chara* ordinarily possess an interesting Chytridiaceous flora.

(b) *Parasites of other water moulds*.—Chytridiaceous fungi are frequently found in old gross water cultures of filamentous water moulds such as *Achlya* and *Saprolegnia*. Species of *Olpidiopsis*, *Woronina*, and *Rozella* occasionally occur in the hyphae, while *Rhizophidium* and *Rhizidiomyces* are often encountered on the oogonia and oospores. The egg-parasitizing forms may generally be detected by the disorganized contents of the attacked structure. It is well to examine carefully all old gross cultures before discarding them, particularly those which have been standing in warm rooms.

(c) *Parasites of microscopic animals*.—Chance alone seems to govern the observer's probability of encountering these forms. In such shallow dishes of algae as have been previously described, numerous rotifers and nematodes will usually develop, and dead individuals of these should be examined with great care, nor should the scum formed along the sides of the dishes be overlooked. Scrapings of *Euglena* scum when placed in shallow dishes and barely, if at all, covered with water, will generally be attacked within a few days by interesting chytrids. Indeed, such cultures are a most prolific source of Chytridiaceous fungi and merit special attention.

2. *Blastocladales*.—The most ubiquitous genus of this order, *Blastocladia*, is primarily an inhabitant of submerged twigs and Rosaceous fruits. On these two substrata it forms white, generally rather crisp and granulated, hemispherical pustules of densely compacted plants. Such pustules ordinarily are composed of a single species, although it is not uncommon to find congeneric forms and even representatives of other orders in company with it.

The collection of fruit-inhabiting fungi is a relatively simple matter. Several hard apples or pears are placed in a galvanized perforated metal container (or ordinary wire screening) and submerged in a likely site. After a month or more the fruits are removed, the surrounding slime (which should be examined for such forms as *Pythiomorpha* and *Pythiogeton*) washed off and samples made of various pustules and filamentous fungi. The material should be examined immediately after collection, since the changing environmental conditions generally induce quick zoospore production. Samples of very minute pustules, as well as the larger ones, should be made, since the former are not always merely immature plants of larger species but often totally different ones. Remarkable variations in the shape of the thallus are found

among species of *Blastocladia*, particularly *B. Pringsheimii*; especially is this true of plants formed in spherical pustules when compared with those occurring in long rows in slits on the surface of the fruit. Species of the Leptomitaceous fungus *Rhipidium* are also commonly found forming pustules on fruits. These may generally be distinguished macroscopically from those of *Blastocladia* by their smooth surface and soft gummy consistency.

3. *Monoblepharidales*.—I have recently given details of the methods used in the collection of these fungi (1933 b). It need only be mentioned here that, in general, species of *Monoblepharis* are commonly found only on sunken undecorated twigs; further, that only rarely does one find them on the twig when examined immediately after collection. In most instances, profuse growth occurs after several days in jars of distilled water maintained at low temperatures (circ. 8°–11° C.). Species of *Gonapodya* are found in company with *Monoblepharis*, or often on twigs at room temperature, or on submerged fruits.

4. *Saprolegniales*.—Members of this order are usually obtained by placing 'bait' of various sorts, both plant and animal, in jars of water containing a small amount of moss or vegetable trash from some aquatic or semi-aquatic site. In recent years a large number of interesting forms have been recovered from the soil. Samples of this are placed in a shallow dish, barely covered with water, and a small piece of bait (the split boiled seed of Russian hemp being most used) placed on the surface in contact with the soil. Since some of these fungi do not possess swimming spores, actual contact of the bait with the soil is essential.

5. *Leptomitales*.—The members of this group are usually found as inhabitants of twigs and fruits, often in company with species of *Blastocladia* and *Monoblepharis*.

6. *Ancylistales*.—These very rare fungi occur occasionally in algal cultures along with Chytridiaceous forms.

7. *Pythiales*.—The algal-inhabiting species of *Pythium* may generally be obtained by placing small amounts of *Spirogyra*, particularly the larger species, in jars of distilled water and leaving them in a cool shaded place. After a few days, the ashen-grey filaments, which invariably develop, should be examined. Other species occur in the soil and in aquatic debris. However, the most prolific source is the roots of crop plants.

The mycelium of the interesting rotifer-capturing form, *Zoophagus*, may often be seen ramifying along the bottom of culture dishes containing algae. It can be readily recognized by the occurrence at short intervals along its length of short peg-like lateral branches, the capturing organs. *Pythiogeton* and *Pythiomorpha* occur commonly in twig cultures which have been kept in the laboratory for many months. Both are also found on Rosaceous fruits.

## FUNGI COLLECTED.

In the following pages is given a list of the fungi collected, with notes on their occurrence, morphological details of especial interest, and in some cases their taxonomy.

## CHYTRIDIALES.

1. ? *PSEUDOLFIDIUM PYTHII* Butler. Parasitic in *Pythium* sp., isolated from heathland sand, Mildenhall, Suffolk, 15 October, 1932.

The fungus produced a marked hypertrophy of the host and a degeneration of the contents, which was characterized by an excessive production of fatty materials. The sporangia, of which one or more were present in a single swelling, were somewhat elliptical,  $15-28\mu$  in diameter by  $10-20\mu$  in height, and possessed a single discharge tube of variable length which penetrated the host wall. The zoospores were not observed, but according to Butler (1907) they are biciliate. Elliptical bodies with smooth thick walls were found associated with the sporangia. These may have been immature resting spores. Fully developed examples of the latter were spherical or subspherical,  $23-27\mu$  in diameter, and possessed a thickened wall the outer surface of which was covered with short, tenuous, radiating spines. Within the content there were numerous oil globules.

This fungus appears to be identical with that figured by Butler, but since the zoospores were not observed, it may be a species of *Rozella*.

2. *PSEUDOLFIDIUM FUSIFORME* (Cornu) Fischer. Parasitic in hyphae of *Achlya* sp., Coe Fen, Cambridge, 29 November, 1932.

3. *WORONINA POLYCYSTIS* Cornu. Parasitic in *Achlya* spp., Barton Mills, Suffolk, 14 November 1932; vicinity of Cambridge, 24 December 1932; January to May 1933.

*Woronina* may become a great pest in laboratory gross cultures of filamentous water moulds.

4. ? (*ROZELLA*) *SEPTIGENA* Cornu. Parasitic in *Saprolegnia* spp. and *Achlya* spp. (*R. simulans* ?), Barton Mills, Suffolk, 14 November 1932.

The form on *Achlya* has been segregated by Fischer as *R. simulans*, but appears to be morphologically identical with that on *Saprolegnia*.

A misconception seems to have arisen in the literature with regard to the genus *Rozella*. As described by Cornu (1872, p. 148), it included four species, described in the following order: 1. *R. Monoblepharidis*; 2. *R. Rhipidii*; 3. *R. Apodyae*; 4. *R. septigena*. The first of these possessed sporangia which completely filled the hypertrophied portion of the host cell and evidently discharged its spores, which were not observed in this instance, through a single pore. The resting spores, which were also formed in the hypertrophied part of the hyphae, were spherical and possessed a thick wall, the outer surface

of which was covered with tenuous radiating spines. A prominent oil globule was present in the content. In *R. Rhipidii* the sporangia of the parasite completely filled those of the host. Here, posteriorly uniciliate zoospores were observed, as well as resting spores which were similar to those of the preceding species. *R. Apodyae* resembled the other two, save that the spines on the resting spore appeared shorter. The fourth species, *R. septigena*, differed from the others in several respects, and was recognized as possessing distinctive characters by Cornu in his introductory remarks concerning the genus. In the main, these aberrant features were (1) the formation of a linear sorus of sporangia from the plasmodial thallus instead of a single one, and (2) the absence in the intercalary portions of the infected hyphae containing these sori of pronounced hypertrophy. Resting spores similar to those formed by the other species were observed and considered to be those of the fungus. The zoospores were described by Cornu as being posteriorly uniciliate, although biciliate 'abnormal' ones were also found. Later, Fischer (1882) definitely indicated that the biciliate type were those normally produced. In this same paper Fischer divided the genus into two groups, the 'sporangium-group' containing Cornu's first three species and the 'septigena-group' containing *R. septigena* and a new species, *R. simulans*, said to be confined to *Achlya*. He thus gave definite emphasis to Cornu's own conception of the dissimilarity of the two groups. This separation was completed in Fischer's monograph (1892), when the two were segregated as separate genera. However, in this splitting Fischer retained the genus name *Rozella*, not for Cornu's first-described species, of which *R. Monoblepharidis* or *R. Rhipidii* might be regarded as the type, but for the aberrant *R. septigena*. The former were placed in a new genus *Pleolpidium*. There seems no justification for this choice of names, even though from the different ciliation of the zoospore the separation of the two groups is necessary.

5. *PLEOLPIDIUM* (*ROZELLA*) *POLYPHAGI* Sparrow\*. Parasitic in pro-sporangia of *Polyphagus Euglenae*, ditch, rear of Ley's School, Cambridge, 3 March 1933.

Sporangia colourless, spherical, completely filling the often markedly swollen pro-sporangia of the host, 20–48  $\mu$  in diameter, possessing at maturity 2–6 prominent papillae, 4–8  $\mu$  in diameter, through which the innumerable minute, posteriorly uniciliate, uniguttulate, narrowly ovoid zoospores, 2–3  $\mu$  long by 1.5–2  $\mu$  in diameter, are discharged. Resting spores not observed.

Material of the host, which had been growing a week or more in the laboratory, was severely parasitized by this fungus (Pl. 14, figs. 19, 20). From the observations of Cornu and Fischer, it has been customary to regard species of *Pleolpidium* and *Rozella* as confined to a single genus of host. The experimental evidence which would validate this is admittedly meagre, and in the present

\* A Latin description of this fungus was given in the Trans. Brit. Mycol. Soc. xviii, p. 215 (1933).

instance entirely lacking. More extensive cross inoculation work will be necessary before any final disposition of the physiological species in these genera can be made.

6. *OLPIDIUM GREGARIUM* (Now.) Schroet. Parasitic in rotifer eggs, Site 4, 4 March 1933.

In dishes of *Euglena* and algae from this site a large number of rotifers soon developed, and on these as well as their eggs there appeared several curious fungi. The first of these parasites occurred only in the ova. One to three ellipsoid sporangia,  $18-35\ \mu$  long by  $17-32\ \mu$  in diameter were formed in a single egg (Pl. 14, figs. 2-4). When occurring alone the sporangia almost completely filled the egg (Pl. 14, fig. 3) and were practically ellipsoid, whereas when more than one were present they were smaller and irregular in outline (Pl. 14, fig. 2). At maturity a single prominent papilla,  $7-10\ \mu$  in diameter, was formed, which protruded through the wall of the egg and through which, upon the deliquescence of its tip, the minute, posteriorly unciliate, uniguttulate zoospores,  $2.5-3\ \mu$  in diameter were quickly discharged. Thick-walled brownish resting spores,  $15-20\ \mu$  in diameter, similar to those figured by Butler (1907) were also found (Pl. 14, fig. 4). These were usually lying loosely in a larger, somewhat spherical structure.

Resting spores and sporangia like the afore-mentioned have also been observed in the eggs of rotifers collected in a shallow pool among the dunes in north Jutland, Denmark, in July 1933.

7. *OLPIDIUM ENTOPHYTUM* Braun. Parasitic in *Cladophora* sp., collected in Hobson's Conduit, Trumpington St., Cambridge, 8 August 1932.

The first of the several algal-inhabiting Olpidioid forms found possessed a smooth-walled sporangium which was nearly spherical, about  $10\ \mu$  in diameter, and at maturity formed a discharge tube about  $8\ \mu$  long by  $3\ \mu$  in diameter, through which the zoospores passed, and before the mouth of which they lay in a motionless mass (Pl. 14, fig. 6). After a period of quiescence each of the spores, which was about  $3\ \mu$  in diameter, detached itself by a tugging motion from its neighbour, initiated ciliary activity, and darted away. The sporangium was smaller than that described by Braun ( $10\ \mu$  in diameter, compared with  $22-25\ \mu$ ).

8. *OLPIDIUM ENDOGENUM* (Br.) Schroet. (?). Parasitic in *Mougeotia* sp., Site 1, 20 December 1932; *Zygnema* sp., Site 1, 3 March 1933.

There were practically no differences in the shape or size of the mature thalli on the two hosts. In both they were ellipsoid and varied from  $15-20\ \mu$  in height by  $27-38\ \mu$  in diameter. The zoospores ( $5\ \mu$  in diameter) were discharged through a somewhat tapering tube,  $5\ \mu$  in diameter, which was slightly inflated just within the algal wall (Pl. 14, fig. 1).

Although these two fungi approximate to Braun's species in size, I am in some doubt whether or not they can correctly be assigned to it. *O. endogenum*,

which has hitherto seemingly been confined to desmids, from Braun's illustrations possesses a much more distinct swelling of the discharge tube, which usually is not sessile on the sporangium as in the British material. A difference of lesser importance is the greater length of the extramatrix part of this tube displayed by the type-species. The present fungi resemble closely the figures of the incompletely known *O. Spirogyrae* Skvortzow and the unnamed species on *Spirogyra* illustrated by Gwynne-Vaughan and Barnes (1927).

A somewhat similar parasite was also found on *Spirogyra* at Site 3 on 8 May 1933. The ellipsoid thalli,  $12\mu$  high by  $25-30\mu$  in diameter, at maturity produced a nearly isodiametric discharge tube,  $17\mu$  long by  $5\mu$  in diameter (Pl. 14, fig. 12). No zoospores were observed. Another *Olpidium*-like fungus was observed in cells of *Euglena* from Site 4, the sac-like sporangium,  $25\mu$  long by  $17\mu$  in diameter, nearly filling the body of the animal. While the minute spores were clearly delimited within the sporangium, discharge could not be induced. While possibly referable to *O. Euglenae* Dang., further data on its method of zoospore discharge and the nature of the spores themselves must be obtained before a final identification is possible (fig. 3, l).

9. ? *PLEOTRACHELUS PETERSENII* Lund. Parasitic in cells of *Zygnema* sp., Site 1, 3 March 1933.

The tube-like thallus of the present material is thick-walled,  $5-7\mu$  in diameter, and possesses short inflated and contorted branches, the ends of which are occasionally sharply truncated and angular in outline (Pl. 14, fig. 5). At maturity the whole one-celled complex is apparently transformed into a sporangium and the zoospores discharged through one or more slender discharge tubes,  $2.5-3\mu$  in diameter, which penetrate the host wall. Since no spores were observed, the resemblance to Lund's fungus may be only a superficial one and the parasite may be a species of *Petersenia* or even a *Lagenidium*.

An examination of the type-material, kindly furnished by Dr. H. E. Petersen and Mr. Lund of Copenhagen, revealed the thalli to be more rotund and less tubular and angular in outline than the British material.

10. *SEPTOLFIDIUM* Sparrow \*. Thallus intramatrix, cylindrical, unbranched, at maturity divided by transverse walls into a series of attached segments, each of which forms a single evacuation tube through which the posteriorly unciliate zoospores are discharged. Resting spores not observed.

*SEPTOLFIDIUM LINEARE* Sparrow \*. Parasitic in *Synedra* sp., Site 1, 3 & 5 September 1932.

Thallus narrowly cylindrical, smooth-walled with slightly tapering ends,  $75-130\mu$  long by  $5-12\mu$  in diameter, divided at maturity into a linear series

\* A Latin description of this fungus was given in the Trans. Brit. Mycol. Soc. xviii, p. 215 (1933).



of truncated conjoined segments,  $8-37\ \mu$  long by  $5-12\ \mu$  in diameter, each of which forms a single broad, abruptly tapering evacuation tube,  $3-5\ \mu$  in diameter, which protrudes from the host cell and through which the numerous zoospores are discharged. The latter spherical,  $3-4\ \mu$  in diameter, with 1-4 spherical or irregularly shaped refractive granules; often forming upon emergence a spherical motionless cluster at the mouth of the discharge tube, ultimately

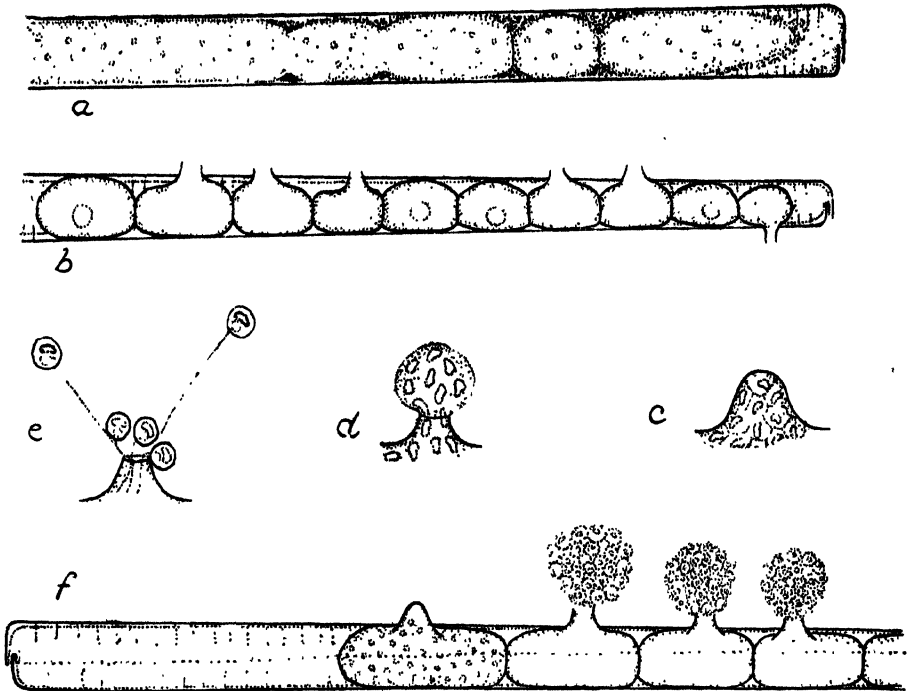


FIG. 1.—*Septolpidium lineare* Sparrow.

- a. Habit of immature thallus in diatom. The tubular body has already become segmented in its more distal part.  $\times 800$ .  
 b. Group of empty sporangia in diatom.  $\times 800$ .  
 c-e. Stages in the discharge of the zoospores.  
 f. Group of sporangia in diatom; the one to the left has not discharged its zoospores. The latter are seen forming a motionless group at the mouth of the discharge tube of the other sporangia.  $\times 800$ .

falling apart and swimming away; sometimes assuming motility directly after emergence.

This interesting fungus was found twice during September in Diatomaceous scum. Although the method of infection of the alga could not be ascertained—though searched for in particular,—large numbers of thalli in various stages

of development were found, and these, together with continuous observations on the formation of the septations, left little doubt as to their method of development. Septation of the thallus appeared to be a progressive process and not a simultaneous one (fig. 1, *a*); nor did the segments thus delimited mature simultaneously. Indeed, in certain cases the sporangia at one end of the thallus had discharged their zoospores before cleavage of the protoplasm had been completed at the other (fig. 1, *f*).

During maturation of the zoospores, which incidentally also seemed to be a progressive process, a broad papilla was formed, the tip of which elongated and protruded from the host cell. No particular orientation of these tubes was noted (fig. 1, *b*) and the fungus undoubtedly gained access to the outside medium by boring through the siliceous wall of the host. Upon initiation of the discharge of the zoospores the broad tip of the tube (fig. 1, *c*) apparently expanded and gave rise to a spherical vesicle (fig. 1, *d*) into which, coincident with its dilation, the tightly packed mass of spores commenced to flow. However, this vesicle soon disappeared, and the majority of the spores emerged singly (fig. 1, *e*). In most instances after emergence they formed a loose motionless cluster at the mouth of the discharge tube (fig. 1, *f*). After a half hour or more this grouping of the spores was abandoned, and they gradually assumed individual movement and darted away. No evidences of the encystment of the swimmers during this motionless stage was ever observed in living or stained material. In a number of instances of discharge, the spores after the disappearance of the vesicle were observed to swim away immediately.

In its general aspects *Septolpidium* bears a close resemblance to *Achlyogeton*, to which genus it was, in fact, at first tentatively assigned. The thallus in the latter fungus consists of a chain of cells, no doubt produced as in *Septolpidium*, each of which becomes at maturity a sporangium provided with a single discharge tube. Further, the posteriorly uniciliate zoospores after emergence form a motionless cluster at the orifice of the tube. In contrast to *Septolpidium*, however, they become encysted, as in a species of *Achlya* or *Aphanomyces*, and after a period of rest emerge from their cysts and swim away. The encystment of the spores in *Achlyogeton* has recently been confirmed by Martin (1927), who in addition found associated with the fungus chains of cells containing loosely disposed, thick-walled, apparently asexually formed resting spores.

In spite of the general similarity of *Septolpidium* to *Achlyogeton*, I consider the lack of an encysted stage in the zoospores to be of sufficient import to warrant generic differentiation.

11. CHYTRIDIUM OLLA Braun. Parasitic on eggs of *Nitella tenuissima* (?) originally collected from Wicken Fen, Cambs., maintained in gross culture at the Botany School; collected 29 October 1932.

One seldom encounters a Chytrid so virulently and extensively parasitic on a particular organ as this. The fungus was very abundant and in some plants destroyed practically all of the eggs.

The extramatrix, sessile, typically urceolate or occasionally ovate sporangia were  $12-37\ \mu$  long by  $6-32\ \mu$  in diameter, their apex being surmounted by a prominent, often umbonate operculum (Pl. 15, figs. 1-3, 5). The latter, which was about  $7-10\ \mu$  in diameter, upon dehiscence allowed the emergence of the compact mass of uniciliate zoospores, each of which was  $5\ \mu$  in diameter (Pl. 15, figs. 6-9). The intramatrix rhizoidal system was of unusual interest. It consisted of a very obvious, stout, thick-walled, unbranched cylindrical portion which was very evident in the host cell in the space between the wall of the oogonium and the contracted disorganized egg mass (Pl. 15, figs. 1, 5). The wall of this cylindrical stalk was often so thick that the lumen appeared as only a thin line (Pl. 15, fig. 3). Either by carefully pulling apart the host material or, rarely, by directly observing the undisturbed egg it could be seen that within its contents the stout stalk branched, tapered, and became distinctly rhizoidal (Pl. 15, fig. 1).

Another interesting feature was the formation on occasional sporangia of remarkable, thick-walled, highly refractive, flame-like outgrowths (Pl. 15, figs. 2-4, 10). In spite of the distinctive appearance of such sporangia they are regarded simply as variations of *C. olla*. Differences in the shape of the operculum were also noted. Generally, this structure was broadly conical, the apex sometimes being umbonate. In other instances it was a convex, watch-glass-like structure of even contour.

Within the disorganized content of the egg were found subspherical or pyriform resting spores borne on a stout rhizoidal system. While no evidence of any sexual process preceding resting-spore formation was noted, a well-defined tube connecting the spore with the surface of the oogonium was often clearly seen (Pl. 15, fig. 11). This may possibly be indicative of previous planogametic activity, the wall of the infecting zygote having disintegrated.

12. *CHYTRIDIUM SCHENKII* (Dang.) Scherff. Parasitic on *Oedogonium* sp., Site 5, 20 September 1932.

This fungus was observed in company with the epiphytic alga *Harpochytrium hedinii*. The sporangia were obpyriform, sometimes curved or irregular,  $13-20\ \mu$  long by  $12-13\ \mu$  in diameter, and possessed an intramatrix spherical base,  $7-9\ \mu$  in diameter furnished with occasional rhizoids (Pl. 15, figs. 15-17). The compact mass of zoospores emerged upon the dehiscence of the convex operculum, which was  $4-5\ \mu$  in diameter. Smooth-walled, intramatrix resting spores about  $12\ \mu$  in diameter were also found (Pl. 15, fig. 15). Plants closely resembling those of *Chytridium pusillum* Scherff. (not Sorokin \*) were sometimes formed (Pl. 15, fig. 16).

\* Sorokin (1883) described from Central Asia a minute *Olpidium*-like fungus found in *Oedogonium* as *Chytridium pusillum*, sp. n. In its present state the species is unrecognizable. Recently, Scherffel (1931) has applied the same binomial to a fungus found on *Characiopsis* which closely resembles *C. Schenkii*, but differs in the shape of its sporangium. The best interests of taxonomy would not be served by continuing Scherffel's binomial, and his fungus is, therefore, termed *Chytridium Scherffeli*, sp. n.—syn. *C. pusillum* Scherffel, non Sorokin (l.c.).

13. *CHYTRIDIUM* sp. (gen. nov. ?). Saprophytic on very old twigs of *Aesculus*, Site 2, 10 August 1932; twigs of *Quercus* sp., Kew Gardens, 1 November 1932.

A number of specimens of this rather interesting fungus were found in gross water cultures of twigs which had been kept many months in the laboratory. The whole plant, including the sporangium, was imbedded in the spongy tissue at the base of pustules formed by other, larger water-moulds (Pl. 15, figs. 21, 24, 26). A few sporangia were with difficulty teased out intact from the substratum (Pl. 15, fig. 25), but usually this treatment resulted in a tearing away of their rhizoidal connections (Pl. 15, figs. 22, 23). For this reason, a proper understanding of the vegetative structures was not obtained.

The sporangia, which were  $17-45\ \mu$  in diameter by  $20-45\ \mu$  long, seemed in general to assume the shape of the confining wall of the cortical cell. Mature specimens were ordinarily provided with a broad, somewhat attenuated beak, which appeared to be extramatrical, and which was surmounted by a smoothly convex or often umbonate operculum (Pl. 15, fig. 26). The zoospores when fully formed were liberated after the dehiscence of the operculum. They were posteriorly uniciliate, uniguttulate, spherical, and  $5-7\ \mu$  in diameter.

Since the nature of the vegetative system of the fungus is at present imperfectly understood, comparison with other forms is impossible. However, from what little is known, it seems distinct from other operculate species, and, while resembling somewhat *Endochytrium* and certain xylophilous forms incompletely described by various investigators, may possibly represent the type of a new genus. A similar fungus has been found in the vicinity of Hanover, N.H., on very old waterlogged twigs of *Betula*.

14. *CHYTRIDIUM* *LAGENARIA* Schenk. Parasitic on *Rhizoclonium hieroglyphicum*, Coe Fen, Cambridge, 29 November 1932.

Material of *Rhizoclonium* which had been kept in jars for several days in the laboratory was severely attacked by a fungus similar to that described by Schenk from *Nitella*.

Briefly, the development of the parasite is as follows:—The zoospore after coming to rest on the host cell encysts, and seems either to retract or drop off its cilium. It then produces a narrow tube, which penetrates the wall of the host. There is soon perceptible just within the host wall a definite swelling, which is formed at the tip of the germ tube. The rhizoidal system itself at first becomes visible as a tenuous outgrowth from the distal part of the swelling (Pl. 16, fig. 1, a). During the subsequent elongation of the rhizoids and the enlargement of the swelling, the body of the zoospore remains relatively small and often appears empty (Pl. 16, fig. 1, b). Ultimately, however, it begins to increase in size and becomes dome-shaped to spherical (Pl. 16, fig. 3). The contents of the thallus possess numerous refractive components of irregular size and shape, those formed in the extramatrical part being notably smaller and usually placed near the entrance to the penetration tube (Pl. 16, fig. 24). While ordinarily the intramatrical system is wholly or

partially obscured by the disintegrating material of the host cell, the extraordinarily stout rhizoids may often be observed near the point of their attachment to the sub-sporangial swelling (Pl. 16, figs. 2, 3, 7). In rare cases rhizoids are apparently lacking (Pl. 16, fig. 4). At maturity the sporangium may attain or exceed the size of the intramatrical swelling, this expansion probably being due to the reception of the contents of the whole thallus. Some sort of wall or plug is undoubtedly laid down at the base of the sporangium to prevent the back-flow of materials, although no such structure was actually observed.

The formation of zoospores may first be detected by the coalescence of the numerous minute oil droplets which are dispersed in the protoplasm. These fuse to form large, regularly placed globules of uniform diameter, around which the cleavage planes of the zoospores ultimately become visible. Occasionally, the walls of certain of the larger sporangia are relatively thick and present a double contour in optical section. If conditions are unfavourable for germination, the sporangia may rest for an unlimited time in the mature condition. Under 'favourable' conditions, the apex of the sporangium opens by the circumscissile dehiscence of an apical operculum of varying convexity. Coincident with this action the wall of the sporangium may often be split and shattered (Pl. 16, figs. 4, 6). The zoospores immediately emerge *en masse* devoid of ciliary action (Pl. 16, fig. 5). Outside they remain motionless for a few seconds near the mouth of the sporangium before assuming individual movement—generally initiated by a trembling motion of increasing intensity. The swimmers are of the usual Chytrid type,  $5\mu$  in diameter, and, save for short periods of amoeboid crawling, glide and spin through the water in a very even, lively fashion.

In older infections, intramatrical, thick-walled resting spores containing one or more prominent oil globules were found (Pl. 16, fig. 24). Very frequently, as in *C. olla*, these appeared connected to the outside of the host cell by a narrow tube. However, no evidences of sexuality preceding the formation of the spores was observed. In this connection, certain observations on the behaviour of the zoospores in hanging drop cultures might be of interest. These, after swimming for a few hours, came to rest, encysted, and lost their cilia. While there were no indications that they ever functioned as planogametes, the motile spores frequently settled down either temporarily or permanently in contact with other quiescent or even germinated ones (Pl. 16, fig. 17). Permanent contact was established ordinarily opposite the point of emergence of the germ tube of the encysted spore (Pl. 16, figs. 18, 19). Merging of the contents of the two, probably made possible by the dissolution of the wall between them, occurred after twelve hours, the protoplasm of the contacting spore flowing into and enlarging the other (Pl. 16, fig. 20). During the next five days there ensued a remarkable development of the rhizoidal system, far more extensive than I ever before observed among unfused Chytrid spores germinating under similar conditions. At the end of this time some of

the thalli possessed contents throughout, including the body of the apical spore. In other instances the latter had enlarged, collected the contents of the whole thallus in it, and assumed the appearance of a sporangium (Pl. 16, fig. 23), while in still others the apical spore remained empty and the contents were accumulated in the more proximal body (Pl. 16, figs. 21, 22).

From the nature of this activity, its end product (an extensive thallus), and the fact that it occurred in a medium practically, if not wholly, devoid of nutriment, I am inclined to regard this conjugation as an attempt by the organism to rejuvenate and prolong its vegetative activity under poor environmental conditions rather than as a sexual process. It was easily observed that the thalli resulting from this fusion possessed greater vigour and longevity than those formed from single spores. The latter were feebly developed and disintegrated within twelve hours.

Other features of interest were exhibited by the fungus. Of the many problems involved in a taxonomic study of the Chytrids, two seem of prime importance and must ultimately be solved before lasting, fundamental work can be accomplished. The first of these is to determine whether or not a single fungus is confined to a particular host, whereas the second is concerned with the morphological and especially the quantitative changes which occur in the same organism when growing on different hosts. A few attempts have been made in the past with parasitic species towards a solution of these problems, but the data accumulated are extremely limited and generally negative. Further, practically no work has as yet been done to determine definitely in cases of apparent host specificity among the Chytrids whether all strains of a species are confined to a single host or whether one strain may not vary somewhat in its virulence under different environmental conditions.

Owing to the relative abundance of the present material a few preliminary attempts at cross-inoculation experiments were done. While the data are admittedly scanty, under the conditions of the experiments certain interesting facts were brought out.

The method used in these tests is, briefly, as follows :—Uninfected filaments of the prospective host were placed in each of five Van Tieghem cells containing filaments of *Rhizoclonium* bearing mature sporangia of the fungus. These filaments had previously been washed gently several times in sterile water before placing in the cells. Another set of five cells containing only the washed filaments of the prospective host were also prepared and placed under identical conditions to serve as controls. Throughout the course of the next few days frequent examinations of both sets were made.

Soon after being placed under these conditions the sporangia of the fungus discharged its spores and many hundreds of these swarmed in the drops among the algal filaments. Two algae were used in these trials, a species of *Spirogyra* and a slender species of *Oedogonium*. The results were all positive, and the morphological characteristics of the fungus when growing on the various hosts are given in the table on p. 435.

TABLE II.—*Showing the morphological variations occurring in Chytridium lagenaria when growing on different hosts.*

Host.	Average diameter of sporangia.	Shape of sporangium.	Average diameter of intra-swelling.	Shape of intra-swelling.	Nature of rhizoidal system.	Diameter of zoospore.	Diameter of operculum.	Diameter of host-cell.
<i>Rhizoclonium hieroglyphicum</i> .	29 $\mu$ (20–35 $\mu$ ) *.	spherical to subspherical.	23.2 $\mu$ (19–30 $\mu$ ) *.	spherical or somewhat depressed.	stout, extensive, much branched.	5 $\mu$ .	6–11 $\mu$ .	60–208 $\mu$ .
<i>Spirogyra</i> sp. ...	8 $\mu$ (6–11 $\mu$ ).	spherical to slightly ovate.	7 $\mu$ (5–10 $\mu$ ).	spherical.	generally slender, poorly developed; not more than two main branches.	5 $\mu$ .	5 $\mu$ .	23–25 $\mu$ .
<i>Oedogonium</i> sp. ...	13 $\mu$ (12–15 $\mu$ ).	spherical to subspherical.	9 $\mu$ (7–10 $\mu$ ).	spherical to subspherical.	none visible.	5 $\mu$ .	5 $\mu$ .	15–18 $\mu$ .

\* Limits of variation.

From a perusal of the table certain interesting facts become apparent. The size and nature of the zoospore remained constant on the three hosts. Further, an intramatrical swelling was always formed and, though varying somewhat in size, was never larger than the sporangium. The latter, while exhibiting striking variations in size on the three algae maintained in general the same shape (Pl. 16, figs. 8-12 on *Spirogyra*; figs. 13-16 on *Oedogonium*). Apparently variations in sporangial size were not coordinated with differences in the diameter of the host cell, for, while the largest sporangia were indeed formed on the alga having the largest cells (*Rhizoclonium*), the smallest were not formed on the most slender filaments (*Oedogonium*), but, rather, on *Spirogyra*. It is further evident that the rhizoidal system underwent marked variation on the three algae, being extremely stout and well developed in *Rhizoclonium*, very sparse in *Spirogyra*, and either so tenuous as to be invisible or entirely lacking in *Oedogonium*.

While these data are scanty they are significant, and would seem to emphasize the necessity of making such studies generally among all parasitic members of the group in order that we may obtain ultimately a proper understanding of the morphological and physiological factors of taxonomic importance.

In considering the affinities of the present fungus certain previously described forms should be considered. In 1858 Schenk (1858 *a*) described as *Chytridium lagenaria* a form found parasitic on *Zygnema*, *Spirogyra*, and *Oedogonium*, which possessed an ovate sporangium and a somewhat larger, laterally expanded, subspherical intramatrical swelling from the whole surface of which rhizoids emerged. The zoospores escaped after the rupturing of the apical portion of the sporangium. In neither the text nor the figures was the possession of an operculum implied. Later the same year (1858 *b*) he described a fungus on *Nitella*, which possessed an intramatrical swelling and a subspherical to urceolate sporangium. Not only were the rhizoids of this form stouter than those figured in the preceding species, but the sporangium was definitely operculate. This form Schenk also placed in *C. lagenaria*, and indicated that by so doing he corrected his previous observations on the zoospore discharge. A considerable variation in the size of the sporangia was noted by him. Although it is not now possible to say that there was ever an operculum on the sporangia of the first-described material, there seems a strong possibility that Schenk was unduly influenced by the prominent subsporangial swelling produced by all his fungi, and that he had, in reality, two different species. One of these (1858 *a*) would now be placed in *Phlyctochytrium*, the other (1858 *b*) in *Chytridium*. The fungus termed *Rhizidium lagenaria* by Dangeard (1889) is very similar to Schenk's species on *Nitella*, and should no doubt be referred to it rather than to *Chytridium inflatum* Sparr., as has been previously suggested (1933 *a*). The sporangia of the last-named fungus are typically distinctly pyriform, although occasionally urn-shaped. Perhaps the British material is in most striking agreement with the fungus



termed *Rhizidium Westii* by Masee (1891). While one cannot agree with this author in his interpretation of the method of development of his fungus, in its morphological features, particularly in the stoutness of the rhizoidal system formed on *Cladophora*, and the apparent fracturing of the sporangium wall, there is a close resemblance. Here, too, marked differences in the size of the sporangium and nature of the rhizoidal system were observed on the two hosts (*Cladophora* and *Spirogyra*). Unfortunately, the data seemed to have been derived, certainly in the parasite of *Spirogyra*, from killed material, and hence accurate observations on the method of zoospore discharge (operculate or inoperculate) are lacking. In spite of the apparent absence of an operculum in *R. Westii*, I feel more certain of the identity of my fungus with it than with the *C. lagenaria* first described by Schenk (1858 a). Possibly the best disposition of these forms for the present would be to place Schenk's fungus on *Nitella*, *Rhizidium Westii*, Dangeard's and the present organism under the binomial *C. lagenaria* pro parte, and to refer the fungus first described by Schenk under this name to the genus *Phlyctochytrium*, if there seems sufficient reason in the future for maintaining the latter genus distinct from *Rhizophidium*.

15. CHYTRIDIUM VERSATILE Scherffel. Parasitic on *Synedra* sp., brook in St. Andrew's St., Cambridge, 8 August 1932; Coe Fen, Cambridge, 2 November 1932.

In both collections the sporangia when mature were obpyriform and possessed a branched intramatrical system at the tip of the conspicuous needle-like penetration tube. In the St. Andrew's St. collection (fig. 3, *g*) the sporangia averaged  $15\ \mu$  in length by  $10\ \mu$  at their greatest diameter, whereas the material from Coe Fen (fig. 3, *t*) never exceeded  $8\ \mu$  by  $5\ \mu$ . The latter resembled to a marked degree the incompletely known *Rhizophidium septocarpoides* Petersen, not only in shape but in the possession of an extramatrical stalk on which rests the base of the sporangium. Certain fungi found on *Tabellaria* sp. at Site 5 may also belong to this species (fig. 4, *a*).

16. CHYTRIDIUM INFLATUM Sparrow. Parasitic on *Oedogonium* sp., Site 5, 20 September 1932.

Only the empty operculate sporangia were found (Pl. 15, fig. 19).

17. CHYTRIDIUM APPRESSUM Sparrow. Parasitic on *Melosira varians*, Site 1, 18 September 1932.

A few examples of this interesting little fungus, hitherto only reported from the United States, were found. The sporangia (Pl. 15, figs. 12-14) were more broadly pyriform than those of the type-material, being  $13-17\ \mu$  long by  $9-10\ \mu$  in diameter, and the zoospores were smaller, seldom exceeding  $3\ \mu$  in diameter. These were discharged after the dehiscence of a very thin-walled convex operculum.

18. *CHYTRIDIUM SPHAEROCARPUM* Dangeard. Parasitic on *Mougeotia* sp., Coe Fen, Cambridge, 6 September 1932; on filaments of *Achlya* sp., Barton Mills, Suffolk, 6 November 1932; on *Spirogyra* sp., Site 1, 6 March 1932.

The organisms growing on the three hosts appeared morphologically indistinguishable. The sporangia were all pyriform and possessed a delicate, sparsely branched rhizoidal system. On *Spirogyra* (fig. 3, *b, c*) they were 8–10  $\mu$  long by 7  $\mu$  in diameter, and the rhizoids extended for a relatively long distance within the host cell before branching. On *Mougeotia* (fig. 3, *d-f*) the sporangia were 9–10  $\mu$  in height by 7–8  $\mu$  in diameter, and branching of the rhizoid occurred close to the inner face of the host wall. On *Achlya* (fig. 3, *a*) they were of uniform size, being 9  $\mu$  in height by 7  $\mu$  in diameter; the rhizoidal system closely resembled that formed on *Spirogyra*. In all these fungi the zoospores were 2.5–3  $\mu$  in diameter and escaped after the dehiscence of a strongly convex operculum.

What may possibly be the same species was found at Site 1 on 18 September 1932 on *Oscillatoria*. Here, the pyriform sporangia were 13  $\mu$  in height by 10  $\mu$  in diameter. Since the discharge of the zoospores was not observed, the identity of the fungus must remain in doubt.

19. *CHYTRIDIUM CHAETOPHILUM* Scherff. Parasitic on *Bulbochaete* sp., Wicken Fen, Cambridge, 1 August 1932; saprophytic on *Typha* pollen (bait), Site 5, 20 September 1932.

In this material, only the spherical sporangia, 7  $\mu$  in diameter, strikingly ornamented with long, tenuous, radiating hairs were observed (Pl. 15, fig. 18). The finding of this species on pollen was surprising, since the form had hitherto been regarded as a parasite of algae, particularly members of the Oedogoniaceae.

In addition to the afore-mentioned Chytrids, several other fungi (which may be species of *Chytridium* or *Rhizophidium*) were incompletely observed.

On the internodal cells of *Nitella tenuissima* (?), originally collected in Wicken Fen, Cambridge, a number of pyriform sporangia, 9  $\mu$  in height by 6  $\mu$  in diameter, each with a prominent, somewhat eccentrically placed papilla, were found. Within the host there was a small spherical absorbing organ about 3  $\mu$  in diameter, which was devoid of rhizoids. No zoospore discharge was witnessed. In general, the fungus resembled *Phlyctidium Chlorogonii* Serb.

A second fungus was found parasitizing a spherical unicellular green alga at Site 4 on 3 March 1933. The large pyriform sporangium was 25  $\mu$  high by 23  $\mu$  in diameter, and possessed a broad apical papilla. The partially obscured intramatrical system appeared to be knob-like. Emergence of the zoospores could not be induced. Sporangia similar to these, but smaller (13  $\times$  10  $\mu$ ) and with a branched rhizoidal system, were also found in the same collection (Pl. 15, fig. 20).

20. *RHIZOPHIDIUM SUBANGULOSUM* (Br.) Rabenh. Parasitic on *Oscillatoria* sp., rear of Ley's School, Cambridge, 13 February 1933.

Infected portions of the *Oscillatoria* filaments were of a greyish cast, and were soon fragmented from the uninfected portions of the alga.

In infecting the host, the spherical body of the zoospore, about  $3\mu$  in diameter, after coming to rest on the apical cell of the alga, produced a broad, slightly tapering filament which elongated and penetrated successive cells. The most fully developed specimens observed possessed a broad obpyriform extramatrical part,  $15-16\mu$  in diameter, which tapered to form an intramatrical 'neck', from the lower part of which arose the branched or unbranched, broadly tubular, often somewhat undulating rhizoidal system (Pl. 17, figs. 1, 2). The latter was  $60-65\mu$  in length.

21. *RHIZOPHIDIUM LAGENULA* (Br.) Fischer. Parasitic on *Melosira varians*, Site 1, 5 September 1932; Site 5, 20 September 1932; Coe Fen, Cambridge, 13 February 1933.

Immature, narrowly spindle-shaped sporangia were found in relative abundance at the three localities (fig. 4, *k-m*). In only one instance was a mature specimen observed.

On *Synedra* and *Melosira* collected in Coe Fen, 6 September 1932, a form was observed (fig. 4, *j, n*) which appears closely related to *R. lagenula*. However, the sporangia, which were  $18-22\mu$  long by  $8-10\mu$  in diameter, were more broadly fusiform, often resting on a broad base. The branched intramatrical system was stout and well developed.

22. *RHIZOPHIDIUM SIMPLEX* (Dang.) Fischer. Parasitic on *Spirogyra* sp., Site 1, 18 September 1932; *Chlorococcum* (?), Site 5, 3 March 1933.

The sporangia of *R. simplex* are narrowly pyriform and vary from  $8-10\mu$  in height by  $6-7\mu$  in greatest diameter (fig. 3, *h, i*). The rhizoidal system is tenuous, unbranched, and of limited extent, seldom attaining a length of more than  $10\mu$ . Upon the deliquescence of the apical papilla the few zoospores,  $3\mu$  in diameter, emerge through the terminal pore. There were also formed spherical, extramatrical, thick-walled resting spores,  $6-7\mu$  in diameter (fig. 3, *r*).

In several instances, internal proliferation of the sporangium appeared to have taken place (fig. 3, *j, k*). Special care was taken to make sure that this condition was not in reality an optical effect produced by several superimposed sporangia. Nevertheless, considering the small size of these structures further observations will be necessary to confirm the occurrence of this phenomenon, hitherto unreported in this genus.

23. *RHIZOPHIDIUM GONIOSPORUM* Scherff. Parasitic on *Tribonema bombycina* forma *minor*, Site 1, 6 March 1933; Site 4, 3 March 1933.

In this interesting fungus the zoospore upon coming to rest on the surface

of the host cell loses its cilium (fig. 2, *a*) and produces a barely perceptible penetration tube which pierces the wall and forms within an extremely delicate, branched rhizoidal system. The body of the spore as it enlarges quickly assumes the citriform shape so characteristic of the mature sporangium (fig. 2, *b*, *d*). This, which rests with its long axis parallel with that of the

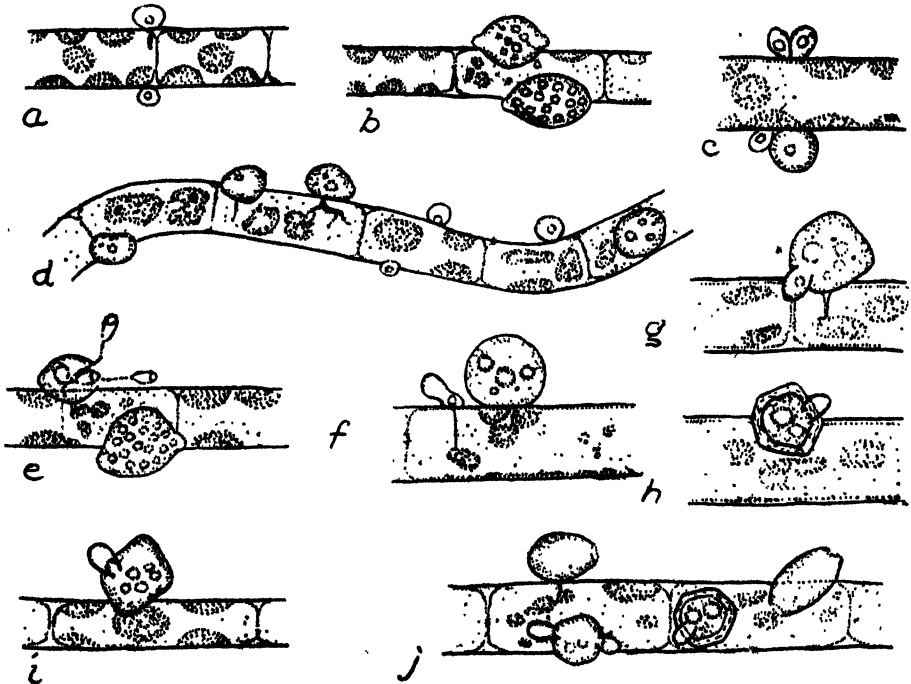


FIG. 2.—*Rhizophidium goniosporum*. Parasitic on *Tribonema*.

- a. Two very young thalli.  $\times 1100$ .
- b. Mature citriform sporangia.  $\times 1100$ .
- c. Early stages in the process of sexual reproduction.  $\times 1300$ .
- d. General appearance of fungus on host.  $\times 1100$ .
- e. Mature and discharging sporangia.  $\times 1100$ .
- f. Male and female (large) thalli.  $\times 1300$ .
- g. Receptive thallus with attached male cell.  $\times 1300$ .
- h. Mature resting spore with empty male cell adherent to it.  $\times 1300$ .
- i. Immature resting spore with male cell.  $\times 1300$ .
- j. Discharged sporangia and resting spores on host.  $\times 1100$ .

algal filament, varies from  $5-7\ \mu$  in height by  $7-10\ \mu$  in breadth. At maturity two lateral, oppositely-placed papillae are generally formed, which upon their deliquescence allow a number of minute, ovate, terminally uniguttulate zoospores to emerge. These are  $3\ \mu$  long by  $2\ \mu$  in diameter (fig. 2, *e*).

The extramatrical resting spores, which vary from  $6-7\mu$  in breadth, are not only of unusual appearance, being polyhedral and generally six-sided in optical section (fig. 2, *h, j*), but are clearly the result of a well-defined sexual process. The latter is similar in its main features to that already described as occurring in this and several other species of the genus, and involves the transference of the contents of a single (occasionally two) small, relatively undeveloped thallus into a larger receptive one.

Owing to the small size and scarcity of the material, few details of the sexual process, particularly in the early stages, have been observed either by Scherffel or myself. What may be very early stages in the conjugation are shown in fig. 2, *c*. Here, the spores have evidently come to rest in pairs. In one instance (fig. 2, *c*, lower) one spore is already markedly larger than the other, whereas in fig. 2, *c*, upper, they are nearly the same size. It is entirely probable that the latter represents the earliest condition: That the spores are at first alike in size and that only in their subsequent rate of growth do they differ. Since the material did not afford opportunity for continuous observations, this sequence awaits confirmation. Such instances as shown in fig. 2, *g, i*, may indicate that the 'male' thallus has been torn from its rhizoidal connections by the enlargement of the receptive plant, or may show that contact with the former had occurred at a relatively late stage in the growth of the receptive thallus. Fig. 2, *f*, might seem to bear out the latter hypothesis. Here, a practically mature spherical 'female' thallus has not as yet made contact with the smaller male structure. It would be interesting to know whether or not in such cases the plants may mature parthenogenetically.

The present material differs in no essential features from that described by Scherffel, save that the zoospores are smaller ( $3 \times 2\mu$ , compared with  $6 \times 3\mu$ ). The rhizoidal system was not observed by Scherffel and, indeed, it is so tenuous as to be nearly invisible.

24. *RHIZOPHIDIUM GLOBOSUM* (Br.) Schroet. Saprophytic on rotifer, *Typha* pollen, Site 2, 8 August 1932; parasitic on *Oscillatoria* sp., Site 1, 18 September 1932.

Under the above binomial may be considered three forms. The first of these was found on the practically empty shell of a rotifer (Pl. 19, fig. 19). There was nothing to indicate that the fungus had caused the death of the animal, although this may possibly have been so. Of the six sporangia found on the shell, five were spherical and  $15-20\mu$  in diameter, whereas the sixth was somewhat elliptical and  $43\mu$  in height by  $37\mu$  in breadth. All had a well-developed rhizoidal system. The zoospores, which were about  $3\mu$  in diameter, were discharged through 2-3 pores. No resting spores were observed.

The second fungus was found on pollen of *Typha*, used to 'bait' a water culture. It occurred after a few days in considerable numbers on the substratum (Pl. 17, fig. 16). The spherical, multiporous sporangia varied from  $12-17\mu$  in diameter; the zoospores were  $3\mu$  in diameter. Within the pollen

grain a delicate, branched rhizoidal system was evident. Such a fungus, while morphologically resembling *R. globosum*, has generally been termed—mainly because of the nature of the substratum—*R. pollinis* (Br.) Zopf. However, from a perusal of Braun's descriptions and figures it is apparent that his fungus possesses more pyriform sporangia, which discharge their zoospores through a single wide apical pore. The most extensive paper on these pollen-inhabiting forms, that of Zopf (1887), unfortunately figured as *R. pollinis* sporangia of both types, and this error has in most cases been perpetuated.

A third Chytrid, found parasitic on filaments of *Oscillatoria*, possessed sporangia 10–12  $\mu$  in diameter, which were at first spherical, but as they matured because of the formation of very prominent papillæ, became more angular in outline (Pl. 17, fig. 3). The sparsely branched rhizoidal system was more delicate than that formed in either the rotifer or pollen grains. The mature zoospores, which swarmed out through the pores formed upon the deliquescence of the papillæ, were similar in size and appearance to those previously described. This fungus appears almost identical with that described by Braun as *R. subangulosum*, differing only in the smaller size of its sporangia and in their lateral position on the host filament. It is indeed a matter of doubt whether Dangeard (1886) and later observers have correctly interpreted Braun's species.

All three of the above forms agree in having (1) practically spherical sporangia, the giant ovate one on rotifer being an exception; (2) approximately the same type and extent of rhizoidal development; and (3) more than one pore formed for the exit of the zoospores. Further, the latter are constantly 3  $\mu$  in diameter. Thus, while these fungi are nearly identical morphologically, whether or not they are physiologically the same is a matter for further study. In no other genus is cross-inoculation work more needed than in *Rhizophidium*, nor more urgently necessary than in the aggregation of forms termed *R. globosum*.

25. *RHIZOPHIDIUM CARPOPHILUM* Zopf. Parasitic on eggs of *Achlya* spp. and *Monoblepharis macrandra*, Site 2, 21 August 1932; eggs of *Dictyuchus monosporus*, Kew Gardens, 1 February 1933.

This ubiquitous species is commonly found in old water cultures of filamentous Phycomycetes. The sporangia, which may occur in great numbers on the host (Pl. 17, figs. 4, 5), are at first spherical, but at maturity because of the formation of a prominent apical papilla become distinctly pyriform. They vary from 7–10  $\mu$  in diameter and possess a single delicate rhizoid, which occasionally may branch in its more distal portion. Spherical, extramatrical, smooth-walled resting spores, 5–9  $\mu$  in diameter are formed in abundance.

26. *RHIZOPHIDIUM SPHAEROCARPUM* (Zopf) Fischer. Parasitic (?) on a nematode, Site 4, 3 March 1933.

The material of this fungus was found on a single cadaver of the worm (Pl. 19, fig. 16, b), where it was associated with *Lagenidium* (Pl. 19, fig. 16, a),

*Saprolegnia* (Pl. 19, fig. 15, *b, d*), and *Aphanomyces* (Pl. 19, fig. 15, *a, c*). All of these fungi were well established within the host and were at the moment exhibiting sporangial activity.

The sporangia and rhizoidal system of the Chytrid (Pl. 19, fig. 16 *b*) closely resemble those of the preceding species. The first-named structures, which were 15–18  $\mu$  in diameter, at maturity liberated their spores (4–5  $\mu$  in diameter) in a compact mass apparently held together by a vesicular structure or imbedded in a gelatinous matrix (Pl. 19, figs. 17, 18). No ciliary action was manifested as they escaped, but after remaining motionless at the mouth of the sporangium for a few moments they assumed individual motility and darted away.

Although occurring on an animal host, the present fungus does not seem morphologically different from that described by Zopf (1884) on *Spirogyra*. I have also found a similar form on nematodes in the United States (1933 *c*).

In addition to these undoubted species of *Rhizophidium*, several fungi were found which were impossible to classify, since the method of zoospore discharge was not observed.

The first of these, found parasitic on *Spirogyra* sp., at Site 1, 18 September 1932, possessed regularly symmetrical pyriform sporangia, 13  $\mu$  high by 10  $\mu$  in diameter, with a prominent apical papilla (fig. 4, *i*). The slender, straight rhizoid was occasionally swollen just beneath the inner face of the host wall. The second fungus (fig. 3, *s*), also found on *Spirogyra* and collected in Coe Fen, Cambridge, on 12 August 1932, possessed a broadly urceolate sporangium, 10  $\mu$  in height by 9  $\mu$  in diameter, which was surmounted by a somewhat laterally placed, wide, slightly extruded pore, the position of which gave a tilted appearance to the whole sporangium. The intramatrical part was unusual, consisting of a cluster of rather stout, stubby digitations. A spherical, thick-walled, extramatrical resting spore, 10  $\mu$  in diameter, with a rhizoidal system similar to that of the sporangium, was also found.

27. PHLYCTOCHYTRIUM (?) BIPOROSUM Couch. Parasitic on *Spirogyra* sp., Site 1, 18 September 1932.

What possibly may be examples of this Chytrid were found in relative abundance on the alga. The ovate, somewhat truncate sporangia, 9–11  $\mu$  in diameter, were provided at maturity with two broad, generally symmetrically placed papillæ of discharge which gave a somewhat bicornate appearance to the whole body (fig. 3, *m-p*). Within the host cell an occasionally slightly inflated unbranched or rarely branched rhizoidal system was observed. Upon the deliquescence of the papillæ the spherical, uniciliate zoospores, 3  $\mu$  in diameter, were liberated. In several instances extramatrical, spherical, thick-walled resting spores (fig. 3, *q*) were found associated with these sporangia and may possibly belong to the species.

The tenuity of the rhizoids and the lack of any pronounced tendency to

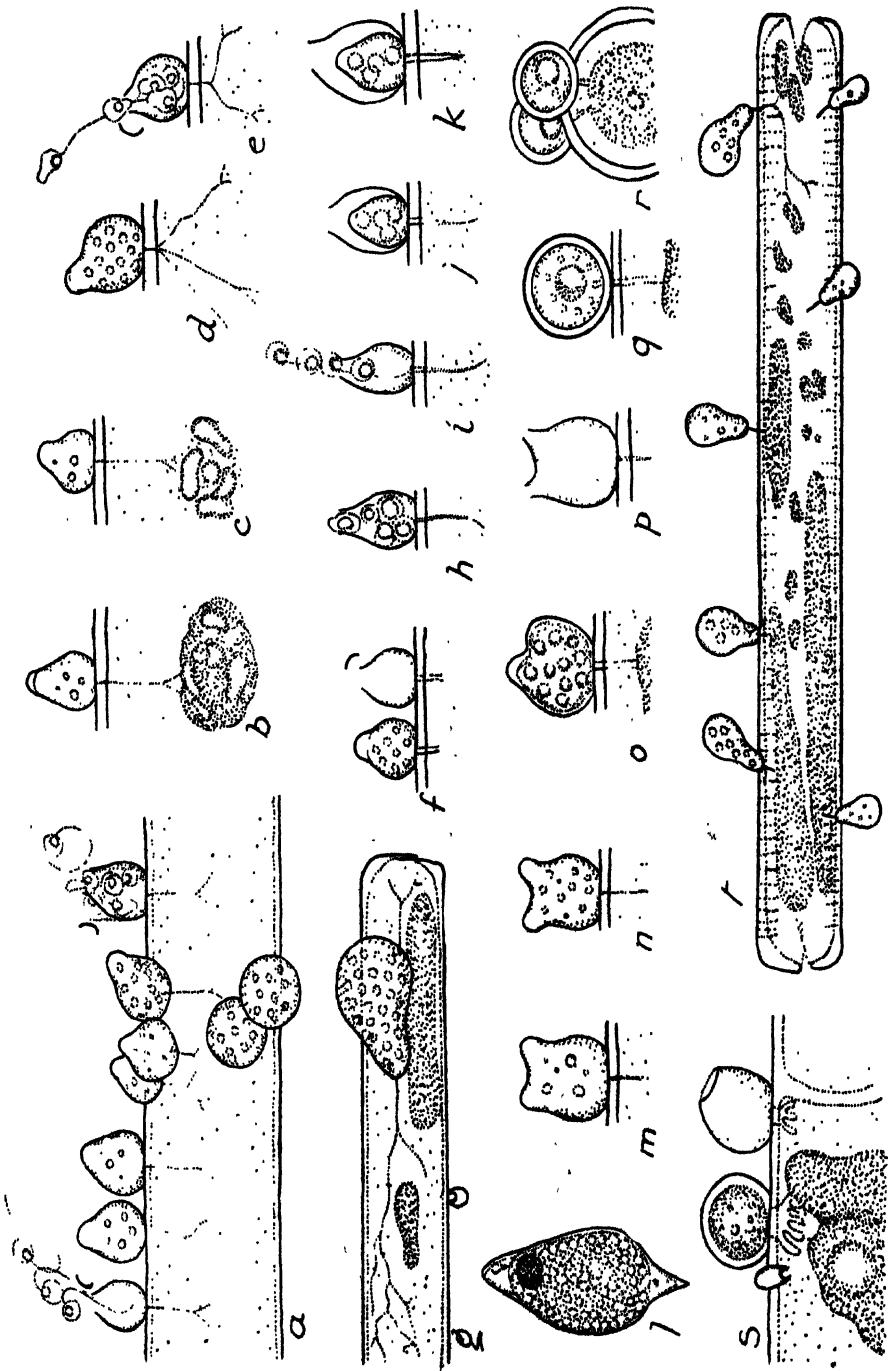


FIG. 3.



## EXPLANATION OF FIG. 3.

- a. *Chytridium ephaerocarpum* on a filament of *Achlya*.  $\times 1100$ .  
 b, c. Same fungus on *Spirogyra*.  $\times 1100$ .  
 d-f. Same on *Mougeotia*.  $\times 1100$ .  
 g. *Chytridium versatile* (?) on *Synedra*.  $\times 1100$ .  
 h, i. Discharging sporangia of *Rhizophidium simplex* on *Spirogyra*.  $\times 1100$ .  
 j, k. Sporangia apparently undergoing internal proliferation.  $\times 1100$ .  
 l. *Olpidium*-like fungus in cell of *Euglena* sp.  $\times 800$ .  
 m-o. Immature sporangia of *Phlyctochytrium* (?) *biporosum*, parasitic on *Spirogyra* sp.  $\times 1100$ .  
 p. Discharged sporangium.  $\times 1100$ .  
 q. Resting spore found associated with sporangia of *P. biporosum*.  $\times 1100$ .  
 r. Resting spores associated with sporangia of *R. simplex* on *Chlorococcum*.  $\times 1300$ .  
 s. Empty sporangium and resting spore of *Rhizophidium* (?) sp. on *Spirogyra*.  $\times 1100$ .  
 t. *Chytridium versatile* (?) on diatom.  $\times 1100$ .

form an intramatrix swelling makes the generic disposition of this material questionable. A discussion of *P. biporosum* has recently been given by the writer (1933 c).

28. *PHLYCTOCHYTRIUM QUADRICORNE* (de Bary) Schroet. Parasitic on *Cladophora* sp., Trumpington St. Brook, Cambridge, 8 August 1932.

The broadly ovate sporangia were about  $13\mu$  broad at the base,  $10-11\mu$  high, and were crowned with four cleft teeth, which surrounded the wide exit pore (fig. 4, o). Within the host there was a spherical portion about  $7\mu$  in diameter which was devoid of rhizoids.

29. *PHLYCTOCHYTRIUM LATERALE*, sp. n. Parasitic on *Spirogyra* sp., Site 1, 24 May 1933.

Sporangia smooth-walled, spherical at first but becoming somewhat flattened and dome-like at maturity,  $12-15\mu$  in diameter by  $10-13\mu$  in height; rhizoidal system consisting of a subspherical enlargement  $9-10\mu$  in diameter by  $6-7\mu$  in height, formed on the inner surface of the host wall beneath the sporangium, provided with a laterally placed, generally branching rhizoid. Zoospores formed within the sporangium, spherical,  $4-5\mu$  in diameter, posteriorly uniloculate with a prominent oil globule; liberated through a pore formed upon the deliquescence of an apical papilla. Resting spores extramatrix, spherical, with a smooth, thick wall,  $12\mu$  in diameter, the content containing a large reserve globule.

*PHLYCTOCHYTRIUM LATERALE*, sp. n. Zoosporangii sphaeroideis v. hemisphaericis, membrana levi munita,  $12-15\mu \times 10-13\mu$ , vesicula infraporangiali intramatrix rhizoides laterales gignente praeditis; zoosporis globosis,  $4-5\mu$  dia., uniguttulatis, 1-ciliatis; sporis perdurantibus extramatrix, uniguttulatis, membrana crassa levi praeditis.

This species differs from other similar congeneric forms in its possession of a single main rhizoidal stalk, which constantly emerges somewhat laterally, rather than centrally, from the subsporangial swelling (Pl. 17, figs. 6–8, 10). The resting spores (Pl. 17, fig. 9) associated with the sporangia probably belong to the fungus, although their germination was not seen.

30. *SCHERFFELIOMYCES PARASITANS*, nom. nov. \*. Parasitic on resting cells of *Euglena* sp., Site 4, 3 March 1933.

*SCHERFFELIOMYCES*, nom. nov.

Syn. *Scherffelia* Sparrow in Trans. Brit. Mycol. Soc. xviii, p. 216 (1933).

Non *Scherffelia* Pascher, in 'Hedwigia', lii, p. 281 (1912).

Zoospores lying free in the water, upon germination producing a narrow tube, the tip of which upon coming into contact with the host cell becomes anchored to the latter by a poorly developed intramatrical system; extramatrical tip of the germ tube expanding and becoming the sporangium, to which is attached the empty cyst of the zoospore. Zoospores posteriorly uniciliate, discharged from the sporangium after the deliquescence of a single papilla. Resting spores extramatrical, thick-walled, with a single appendicular cell, apparently formed in the same manner as the sporangia.

*SCHERFFELIOMYCES PARASITANS*, nom. nov.

Syn. *Scherffelia parasitans* Sparrow in Trans. Brit. Mycol. Soc. xviii, p. 216 (1933).

Sporangium at first lachrymose, becoming spherical or subspherical at maturity, resting in the concavity formed by the collapsed host cell, 17–22  $\mu$  in diameter, joined by a narrow tube of varying length to a spherical cystospore, 2.5–3  $\mu$  in diameter; with a barely perceptible, single, short, unbranched intramatrical tube; contents at first colourless, at maturity charged with orange oil droplets. Zoospores minute, innumerable, spherical or ovoid, 2–3  $\mu$  in diameter with a single orange globule; emerging in a compact mass from the broad mouth of the sporangium and remaining for a few seconds at the orifice, the mass then becoming disorganized as the spores assume motility. Resting spores spherical or ovoid, thick-walled, brownish, 8–10  $\mu$  high by 10–14  $\mu$  in diameter, attached by a narrow, often somewhat curved tube to a single cystospore, 3  $\mu$  in diameter; germination not observed.

This exceedingly interesting little fungus appeared in relative abundance in material of *Euglena* left in Petri dishes in the laboratory for several days. Its development, which exhibited a rather unusual variation of the basic *Chytridium*-type, was as follows:—

The zoospores, after escape from the sporangium, did not come to rest directly on the surface of the host, but lay motionless in the medium and encysted. Upon germination there was produced a narrow tube, the tip of

\* A Latin description of this fungus was given in the Trans. Brit. Mycol. Soc. xviii, p. 217 (1933), and 'Mycologia', xxvi, p. 377 (1934).

which made contact with the host cell. This tube soon became anchored to the *Euglena* by a small lachrymose appressorium on the distal surface of which there was produced a peg-like or often knob-like intramatrical structure (Pl. 18, figs. 14–17). Further growth involved not the enlargement of the spore body itself, but the expanded extramatrical tip of the germ tube which had first functioned as an anchoring organ. This continued to enlarge (Pl. 18, figs. 18–20), and ultimately became a spherical or subspherical sporangium, which often appeared imbedded in the cup-like cavity formed by the now collapsed and discoloured *Euglena* cell (Pl. 18, fig. 22). Occasionally, a series of intramatrical digitations seemed to anchor the sporangium to the host (Pl. 18, fig. 21).

The content of the sporangium was at first colourless, but as it matured became charged with minute, evenly dispersed droplets of orange-coloured oil. These in turn, as maturation continued, coalesced to form larger droplets until at maturity the protoplasm possessed numerous regularly placed, conspicuous, coloured globules. Attached to the sporangium, which varied from 17–22  $\mu$  in diameter, were the empty cyst and germ tube of the zoospore (Pl. 18, figs. 22, 27). Upon the deliquescence of a rather broad, slightly erumpent apical papilla which had developed during maturation, the contents moved out in a compact mass seemingly surrounded by a vesicle (Pl. 18, fig. 23). After a short period of rest before the orifice (Pl. 18, fig. 24), the spores gradually fell away from each other and assumed either an amoeboid (Pl. 18, fig. 26) or a ciliary type of movement (Pl. 18, fig. 25). There seemed some evidence for the assumption that some sort of vesicle was present around the emerging spores, for in one instance during discharge, for some unknown reason, the mass was ruptured and the individuals floated out into the medium only at the point of rupture. Many hundreds of spores were produced by a single sporangium. These were spherical, rarely ovoid, 2.5–3  $\mu$  in diameter, although occasional examples reached 5–6  $\mu$ , were posteriorly uniciliate, and possessed a small spherical orange-coloured globule. They assumed a rapid darting and hopping motion, which often alternated with prolonged periods of very pronounced amoeboid activity (Pl. 18, fig. 26).

Spherical or ovate, extramatrical resting spores, often with a somewhat flattened base were found in limited numbers (Pl. 18, fig. 28). These were 8–10  $\mu$  in height by 10–14  $\mu$  in diameter, and possessed guttulate contents within a moderately thickened, smooth, light brown wall. Each was attached to an empty cystospore, 3  $\mu$  in diameter, by a slender, straight or slightly curved process. The intramatrical part appeared peg-like. While no early stages in the formation of these resting spores were observed, it appeared that they had undergone the same method of development as the sporangia. Further, from a comparison of the sizes of the attached cystospores (3  $\mu$ ) and the zoospores (2.5–3  $\mu$ ) it seemed improbable that any copulatory process involving motile gametes had preceded resting spore formation. It is possible, however, that a type of sexual reproduction similar to that of *Zygorhizidium*

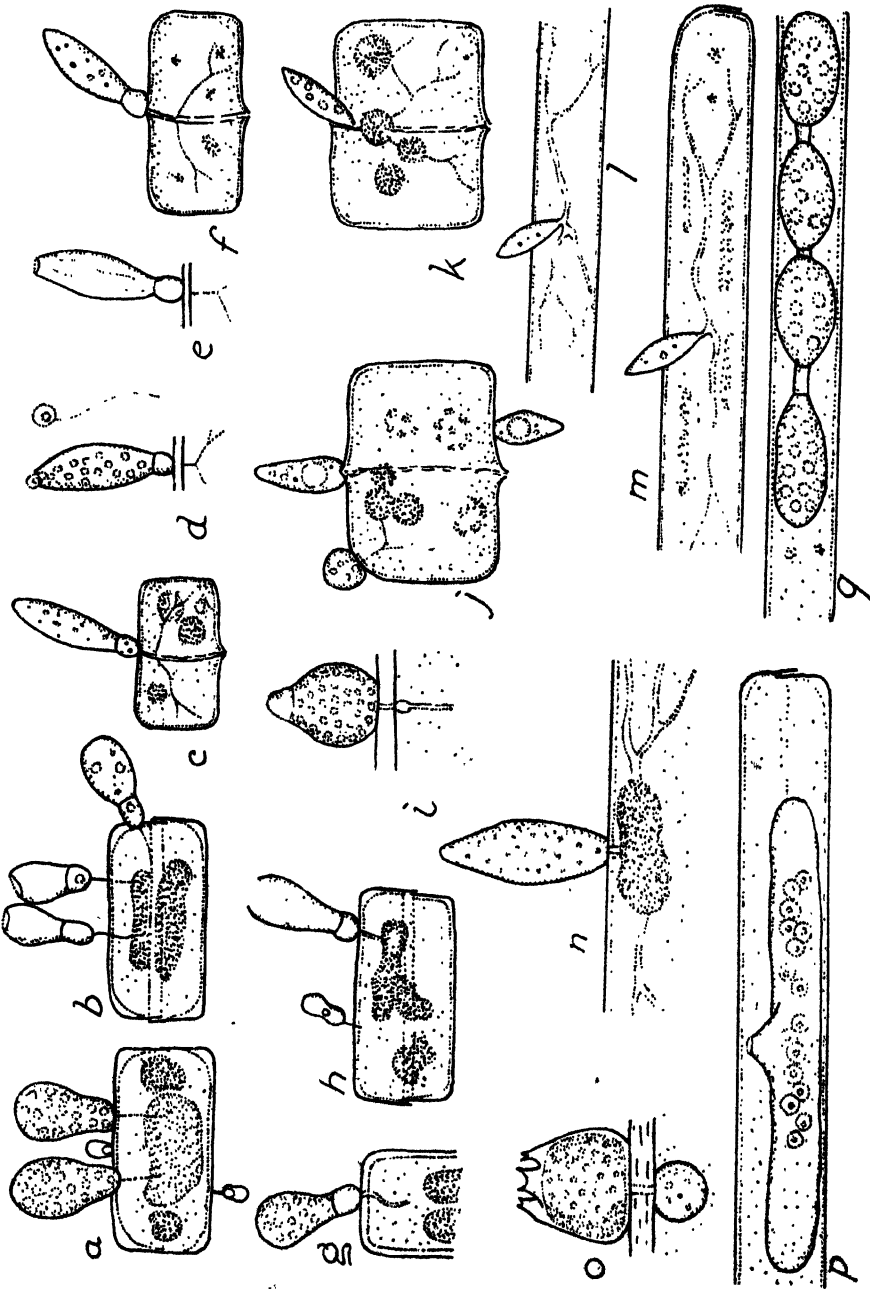


FIG. 4.

## EXPLANATION OF FIG. 4.

- a. Sporangia of *Chytridium versatile* (?) on *Tabellaria*. ×1100.
- b, g, h. Sporangia of *Podochytrium clavatum* on *Tabellaria*. ×1100.
- c, f. Immature sporangia of *Podochytrium lanceolatum* on *Melosira*. ×800.
- d. Discharging sporangium and zoospore. ×800.
- e. Empty sporangium. ×800.
- i. Sporangium of Chytrid on *Spirogyra*. ×1100.
- j, n. Broadly fusiform sporangia of *Rhizophidium lagenula* (?) on *Melosira*. ×1100.
- k, l, m. More typical, narrowly fusiform, immature sporangia: k, on *Melosira*; l, m, on *Synedra*. ×1100.
- o. Mature sporangium of *Phlyctochytrium quadricorne* on *Cladophora*. ×1100.
- p. Discharged sporangium of *Ectrogella monostoma* on *Synedra* (?). A few quiescent zoospores are shown within the sporangium. ×800.
- q. *Myzocytium*-like fungus in diatom. ×1100.

may have occurred. The unique method of development exhibited by *Scherffeliomyces* clearly entitles it to generic distinction.

At least two other fungi have been previously described which may be allied to *Scherffeliomyces*. The first, and most doubtful, was reported by Archer (1867) in describing a new fungus termed *Chytridium Barkerianum*. From the lack of figures and significant notes on its method of development, the fungus is difficult to visualize. As described by Archer, the body of the sporangium is somewhat flattened, concave, and composed of four prominent, broadly rounded, equal lobes. From the centre of the concave upper portion a slender, vertical, hyaline process arose which was terminated by a minute knob. The whole structure was sometimes observed to be anchored to the substratum by an intramatrical rhizoidal system. The zoospores escaped from the apices of the lobes. Neither the ciliation nor size were given nor were the dimensions of the sporangia included. It seems very possible that in this species we have a type of development similar to that of *Scherffeliomyces*, the terminal knob being the cyst of the zoospores. In the shape of the sporangium it differs markedly from *S. parasitans*.

The second, better-known, fungus has been described by Zopf (1884) as *Rhizidium appendiculatum*. From both description and figures, the development is very similar. The sporangia of Zopf's species, are, however, pyriform, colourless, and the resting spore is distinctly apiculate. While assigned by Fischer (1892) and later monographers to *Rhizophidium*, it might better be placed in *Scherffeliomyces*. The binomial *Scherffeliomyces appendiculatus* (Zopf), comb. nov., is, therefore, applied to it.

31. *PODOCHYTRIUM CLAVATUM* Pfitzer. Parasitic on *Fragellaria* sp., Site 5, 20 September 1932.

In dishes of vegetable trash from Site 5, there developed after some weeks a large number of *Fragellaria*. The fungus appeared shortly thereafter in

considerable numbers on the diatom. Its sporangia (fig. 4, *b*, *g*, *h*) were typically clavate, 5–8  $\mu$  in diameter by 10–12  $\mu$  in height, with a basal, cup-like, sterile part, 2.5–3  $\mu$  in diameter, which was sessile or occasionally borne on a short needle-like stalk. Emerging from the distal portion of the latter there could be occasionally discerned within the host cell a delicate, branched rhizoidal system. Posteriorly uniciliate, uniguttulate, spherical zoospores, 2.5–3  $\mu$  in diameter, were formed, and emerged from the sporangium upon the deliquescence of a broad apical papilla.

32. *PODOCHYTRIUM LANCEOLATUM* Sparrow \*. Parasitic on *Melosira varians*, Site 1, 26 December 1932.

Sporangium smooth-walled, colourless, lanceolate, 8–10  $\mu$  in diameter by 20–25  $\mu$  in height, tapering at each end to 3–4  $\mu$ , resting upon a sterile cup-like or occasionally knob-like base, 4–5  $\mu$  in diameter, with a single needle-like intramatrical stalk which gives rise to a few sparsely branched rhizoids at its tip. Zoospores spherical, uniguttulate, posteriorly uniciliate, 3–4  $\mu$  in diameter, discharged successively from the narrow apex of the sporangium through a small pore formed by the deliquescence of a papilla. Resting spores not observed.

This interesting fungus was encountered in limited numbers and the stages in its development were not observed. It differs strikingly from the only other congeneric form—*P. clavatum*—in the lanceolate shape of its sporangium (fig. 4, *c-f*). The whole plant often appears tilted, due, no doubt, to the fact that the parasite seemed to have gained entrance to the alga in the region of the juncture of the two valves. In superficial aspect it was not unlike specimens of *Rhizophidium lagenula*. Infected cells were readily recognized by the green, disintegrated appearance of the chloroplasts.

33. *RHIZIDIOPSIS EMMANUELENSIS* † Sparrow ‡. Parasitic on *Melosira varians* and *Nitzschia* (?) sp., Site 1, 7 March 1933.

#### *RHIZIDIOPSIS* Sparrow.

Zoospore, upon coming to rest on the host cell, encysting and producing an intramatrical rhizoidal system; forming a broad extramatrical germ tube which enlarges and becomes, with the cystospore, the sporangium. Zoospores posteriorly uniciliate, fully formed within the sporangium and discharged

\* A Latin description of this fungus was given in the Trans. Brit. Mycol. Soc. xviii, p. 216 (1933).

† So named not only to recall a site exceedingly rich in all types of aquatic fungi—Chapman's Garden,—but also to express my thanks in an all too inadequate manner to the Master and Fellows of Emmanuel College, Cambridge, for their many kindnesses during the progress of this investigation.

‡ A Latin description of this fungus was given in the Trans. Brit. Mycol. Soc. xviii, p. 216 (1933).

after the deliquescence of a papilla. Resting spores extramatrical, thick-walled; producing a sporangium upon germination.

*RHIZIDIOPSIS EMMANUELENSIS* Sparrow.

Sporangium smooth-walled, pyriform or clavate,  $6-12\mu$  long by  $5-10\mu$  in diameter, the long axis generally parallel with that of the algal filament; attached by its narrower end to, and continuous with, the rounded cyst of the zoospore, which is  $3-4\mu$  in diameter; forming 4-12 or more zoospores,  $3-4\mu$  in diameter, which at maturity are discharged through a single apical pore. Resting spores spherical or somewhat flattened, thick-walled,  $4-4.5\mu$  in diameter, surrounded by a dark brown, rough incrustation; upon germination producing a sporangium.

The developmental features of *Rhizidiopsis* (Pl. 18, figs. 1-4) present another variation of the *Chytridium*-type and resemble closely those of *Podochytrium*. However, in contrast, at no time in either mature or discharged sporangia (Pl. 18, figs. 5-7, 9, 11, 12) could traces of a sterile basal portion be found. Rather, the contents of both basal and distal parts produced zoospores. The relatively small resting spores (Pl. 18, fig. 8) appeared as rusty, spherical or flattened structures on empty or nearly empty algal cells. Generally, no intramatrical system of any kind could be observed. These spores readily germinated after being in the laboratory for a few hours. In this process (Pl. 18, figs. 10, 13) a small sporangium, never more than  $8\mu$  long by  $4\mu$  in diameter, was extruded from the main body of the spore. While the method of formation of these resting structures was not observed, from their small size it would seem that they were formed from a single zoospore which had come to rest on the alga, encysted, and surrounded itself with a stout protective wall.

34. *ENTOPHLYOTIS APICULATA* (Br.) Fischer. Parasitic on resting cells of *Euglena* sp., Site 4, 3 March 1933.

Several specimens of what is probably this fungus were found. The broadly pyriform body of the sporangium, which was about  $13\mu$  in diameter by  $14\mu$  high, was only partially immersed in the host, the narrow apex extending through the wall of the substratum. At maturity the zoospores, which were posteriorly uniciliate and  $2.5-3\mu$  in diameter, emerged in an amoeboid manner through a pore formed by the deliquescence of the tip of the sporangium. After resting for a few moments before the opening, they initiated a violent jerking soon succeeded by a hopping motion, produced by a strong flexing of the cilium, which quickly carried them away (Pl. 14, fig. 7). Other more symmetrical sporangia,  $14-16\mu$  in diameter by  $16-18\mu$  high, were also found in the same material (Pl. 14, figs. 8, 9). In none was there evidence of an intramatrical rhizoidal system, and, since the material was growing in company with other forms which I wished to study further, I was unwilling to remove the dense chlorophyll of the host cell with alcohol to determine this point. Hence, there remains the possibility that these are species of *Olpidium*.

35. *ENTOPHLYCTIS CIENKOWSKIANA* (Zopf) Fischer. Parasitic on *Spirogyra* sp., Wicken Fen, Cambs., Streighton, Cambs., 1 August 1932; *Cladophora* sp., Trumpington St., Cambridge, 3 August 1932; *Vaucheria* sp., Streighton, Cambs., 18 September 1932; *Oedogonium* sp., Site 5, 20 September 1932.

Since specific differences in this genus are at present founded on very questionable characters, for the purposes of this paper the fungi found on these various hosts will be described under the binomial *E. Cienkowskiana*.

In the collections from Wicken Fen and Streighton, the fungi on *Spirogyra* were practically identical, save that the Chytrid from the former locality possessed more narrowly pyriform sporangia and more elliptical resting spores. The sporangia of the Wicken Fen material (Pl. 14, fig. 13) were  $17\ \mu$  in height by  $12\ \mu$  in diameter, the resting spores  $15 \times 12\ \mu$ . In the fungus from Streighton (Pl. 14, figs. 16, 17) the sporangia were  $12\text{--}21\ \mu$  in diameter by  $14\text{--}22\ \mu$  in height, and the resting spores practically spherical and  $14\text{--}15\ \mu$  in diameter; further, the rhizoids were much stouter and more profusely branched. Both forms agreed in having rhizoidal systems arising from a single basal stalk. The fungi on *Vaucheria* and *Oedogonium* were identical in every respect with that of the parasite of *Spirogyra* from Wicken Fen.

On *Cladophora*, the sporangia were practically spherical (Pl. 14, fig. 18) and varied from  $8\text{--}10\ \mu$  in diameter. In the nature and mode of attachment of the rhizoids this organism differed markedly from the fungi previously described. These emerged from several points on the lower half of the sporangium, rather than from a single main trunk, and were delicate and practically isodiametric throughout. Another, perhaps less distinctive feature, was its method of zoospore discharge. In the other forms, the spores, after passing out of the sporangium, formed at the mouth of the discharge tube a motionless compact mass (Pl. 14, fig. 14) which persisted for a few seconds before 'bursting' apart (Pl. 14, fig. 15). Immediately following, the spores assumed motility. In the *Cladophora* fungus, on the other hand, the spores emerged individually from the discharge tube and swam away at once (Pl. 14, fig. 18). Further, this form produced a smaller number of spores in each sporangium. The resting spores were not observed. Considering these differences, it is possible that the Chytrid on *Cladophora* is more nearly allied to *E. rhizina*—a species in which the rhizoids emerge from several points on the sporangium—than to *E. Cienkowskiana*.

What may be another species of the genus, possibly distinct from other congeneric forms, was found on material of *Spirogyra* collected at Site 5, 20 September 1932. The sporangia were broadly pyriform,  $16\text{--}17\ \mu$  in diameter by  $20\text{--}21\ \mu$  in height, and possessed at maturity a short, stout discharge tube, which pierced the host wall (Pl. 14, fig. 10). From the surface of the lower third of the sporangium two oppositely placed rhizoids emerged, which branched and extended for a short distance in the host cell. All efforts to induce discharge of the zoospores were fruitless, and it remains a question whether the form is a species of *Entophlyctis* or *Endochytrium*. Discharged



sporangia (Pl. 14, fig. 11) showed no evidences of opercula. Immature stages of a parasite closely resembling *Entophlyctis bulligera* were observed on material of *Bulbochaete* collected in Wicken Fen, 1 August 1932 (Pl. 15, fig. 18).

36. *CLADOCHYTRIUM REPLICATUM* Karling. Saprophytic on leaves of *Elodea*, Site 2, 6 August 1932; Wicken Fen, 9 September 1932; decayed grass leaves, ditch, rear of Queens' College, Cambridge, 11 October 1932; decayed grass leaves, Site 5, 20 September 1932; decayed grass leaves and stems, Kew Gardens, 1 November 1932.

Karling's excellent paper (1935), giving details of the cultivation of this Chytrid on artificial media, is of unusual interest. The fungus is probably widespread both in the United States and Great Britain.

37. *NOWAKOWSKIELLA ELEGANS* (Nowak.) Schroet. Saprophytic on leaves of *Elodea*, Wicken Fen, Cambs., 9 September 1932; Site 2, 2 October 1932; on decayed grass leaves, ditch, rear of Queens' College, Cambridge, 11 October 1932.

In the material on *Elodea* from Site 2, rather thick-walled bodies were formed (Pl. 17, fig. 17), which, while resembling in shape the apophysate sporangia, contained a number of large spherical oil globules about  $6\mu$  in diameter. Since the latter seem too large to be the globules of the zoospores, and considering the thick walls surrounding the whole structure, it is possible that these thick-walled bodies may be temporary resting sporangia or immature resting spores.

*Nowakowskiella* appears to be relatively common in the vicinity of Cambridge, especially on old leaves of *Elodea*. It may often be recovered from gross cultures by baiting them with pieces of boiled grass culms.

38. *POLYPHAGUS EUGLENÆ* Nowak. Parasitic on the temporary resting cells of *Euglena* sp., ditch, rear of Ley's School, Cambridge, 7 February 1933; Site 4, 3 March 1933.

This exceedingly interesting and beautiful Chytrid developed extensively after two to three days in Petri dishes of *Euglena* scum maintained in the laboratory. It occurred in association with *Scherffeliomyces* and various other fungi. Since the morphology is so well known from the excellent researches of earlier investigators, there seems no reason for including it here, save in one particular, namely, the character of the outer wall of the resting spore. It will be recalled that, in typical material of *P. Euglenæ*, this wall possesses short bullations over its surface.

In the present material, which was maintained in the laboratory for over a month, of the many hundreds of resting spores observed only a very few were found to be ornamented, the vast majority being smooth-walled. As Nowakowski (1876) has pointed out, the occurrence of ornamented and smooth-walled 'races' in this species is in need of thorough investigation. Certainly

the two spores are very different, not only with regard to the wall, but in the shape of the whole structure. In the Cambridge fungus they were very definitely elliptical in outline (Pl. 14, fig. 21) with truncated ends. In material of this species collected in Denmark in July 1933, large numbers of the bullate-walled resting spores were formed to the total exclusion of the smooth-walled variety. In the great majority these spores were practically spherical (Pl. 14, fig. 22). No significant differences in size separated the two types, although the smooth-walled ones were somewhat smaller ( $16-29\ \mu$  long  $\times$   $12-20\ \mu$  in width, compared with  $23-42\ \mu$  in diameter).

Since earlier investigators found both types of resting spores mixed in their cultures \*, it seemed logical to assume—considering the similarity in other respects of the two fungi—that they were the same species. While Nowakowski seems in general to have adopted this attitude in his 1876 paper, mainly because of the absence of data on the nature of the wall in successive generations of the same plant, he did suggest the possibility, as has been stated, of the presence of two distinct races. It is of interest to note that in his 1878 paper, written in Polish (1878), the smooth-walled form is termed *P. Euglenae* var. *minor*. I am inclined to believe that further researches will establish the fact that there are two distinct species involved, which may occur together or separately, rather than Wager's (1913) contention that they are produced by the same species under varying conditions of nutriment.

39. ? RHIZIDIUM spp. Saprophytic on decaying vegetable debris, Site 5, 20 September 1932.

Two fungi of doubtful affinities, but possibly related to *Rhizidium*, were found in pieces of vegetable debris from Site 5. The first of these possessed a pyriform sporangium  $20\ \mu$  high by  $13\ \mu$  in diameter (Pl. 17, fig. 12), which was provided at its apex with a broad, tapering, slightly bent discharge tube about  $5\ \mu$  in diameter by  $15\ \mu$  in length. The whole structure rested on a short thick-walled stalk, which gave rise to two oppositely placed secondary branches. These in turn branched and rebranched, forming a fairly extensive rhizoidal system, the tips of which made contact with pieces of the decaying vegetable matter. While the presence in the contents of regularly placed spherical oil globules indicated that the sporangium was mature, all efforts to induce zoospore discharge were futile.

The second (Pl. 17, fig. 11) was of a somewhat different character and of more doubtful affinities. The central body was spherical or occasionally dome-shaped, and varied from  $14-18\ \mu$  in height by  $13\ \mu$  in diameter. From opposite sides of this structure, which undoubtedly was formed from the expanded body of the zoospore, there were produced two or more rather stout

\* In de Bary's slides of this fungus in the British Museum (N.H.), labelled 'Mai, 1876, glyc. Nowakowski', both types are present in the same mount. Incidentally, this material can certainly be considered a co-type of the fungus.

main axes of an extensive rhizoidal system which ramified throughout the debris. The contents possessed a number of irregularly shaped, colourless, refractive bodies. Here, again, the production of zoospores was not observed, and the affinities of the fungus could not be determined, although in certain features it strongly resembled *Polyphagus*.

### BLASTOCLADIALES.

40. *BLASTOCLADIA RAMOSA* Thaxter. Saprophytic on fruit of apple, Site 3, 29 November 1932.

This species was found only once. The basal portion consisted of a narrowly cylindrical main axis,  $130\ \mu$  long by  $33\ \mu$  in diameter, which at its apex branched and rebranched, forming a number of secondary branches, on the tips of which the reproductive organs were formed. The whole plant was about  $460\ \mu$  in length (Pl. 20, fig. 7). The sporangia, which were oval or broadly fusiform, varied from  $60\text{--}70\ \mu$  in length by  $20\text{--}25\ \mu$  in diameter. The colourless, relatively thin-walled, narrowly clavate, basally truncated resting spores were  $40\text{--}50\ \mu$  in length by  $13\text{--}20\ \mu$  in diameter.

41. *BLASTOCLADIA ROSTRATA* Minden. Saprophytic on twigs of *Aesculus* sp., Site 3, 9 September 1932.

Several tufts of this fungus were found growing in company with *Rhipidium* and *Blastocladia Pringsheimii* (Pl. 20, fig. 14). The whole thallus, including the hold-fasts, was over  $500\ \mu$  in length, and consisted, as in the preceding species, of a narrowly cylindrical basal axis,  $140\text{--}150\ \mu$  in length by  $15\text{--}25\ \mu$  in diameter, which in its distal portion branched and rebranched in a dichotomous or pseudo-dichotomous manner. The tips of the branchlets bore broadly fusiform, somewhat attenuated, basally truncate sporangia,  $47\text{--}55\ \mu$  in length by  $17\text{--}20\ \mu$  in greatest diameter ( $10\ \mu$  at the base). The zoospores, which emerged from the sporangium in a compact column before dispersing, were spherical, posteriorly uniloculate, and about  $10\ \mu$  in diameter. The brown, punctate, thick-walled resting spores, which were borne in the same manner as the sporangia, were somewhat ellipsoid with a prominent apical beak, and rested on a broad, truncated, slightly elongated base. They were  $30\text{--}37\ \mu$  in length by  $15\text{--}20\ \mu$  in greatest diameter ( $10\text{--}15\ \mu$  at the base). Unbeaked resting spores were also occasionally formed.

42. *BLASTOCLADIA PRINGSHEIMII* Reinsch. Saprophytic on twigs of various types; apples; throughout the year, Sites 1, 2, 3.

This ubiquitous species may be obtained at any time in any quantity at all the sites in the vicinity of Cambridge.

Included under this binomial there are grouped plants which superficially exhibit a wide variation, but which generally have in common cylindrical

sporangia at least five times (usually more) longer than wide, and brown, thick-walled, punctate, oval or spherical, sometimes somewhat elongated resting spores with a rounded apex and truncated base.

As has been suggested, the thallus presents a remarkable series of variations, a description of which cannot be entered into at this time. It has been noted, however, that when plants occur in rounded pustules on the surface of the substratum they exhibit more frequently the somewhat arborescent habit with terminally swollen tips than when growing in narrow slits on the fruits. In the latter case the tree-like habit is lost, the termini are only slightly swollen, and the plants assume a more open ramose character. In the present material (Pl. 20, fig. 5), the sporangia varied from 80–160  $\mu$  in length by 15–30  $\mu$  in diameter; the resting spores were 32–60  $\mu$  long by 22–35  $\mu$  in greatest diameter, occasional ones being nearly spherical,  $32 \times 30 \mu$ , while others were very elongate,  $50 \times 25 \mu$ .

It is evident that a considerable amount of work must be done before all the forms now grouped under *B. Pringsheimii* can be definitely proven to belong to one species. The type shown in Pl. 20, fig. 5, and the branched variants, the writer regards as most nearly fitting the usual concept of the species.

43. *BLASTOCLADIA GLOMERATA*, sp. n. Saprophytic on sunken twigs of *Aesculus*, Site 2, 24 December 1932; 20 April 1933.

Whole plant, exclusive of hold-fasts and sterile setae, 693–920  $\mu$  in length, with stout smooth walls up to 10.4  $\mu$  thick; basal cell stout, very broad at the base, 312–364  $\mu$  in length by 104–162  $\mu$  in diameter, rarely unbranched, usually giving rise distally to 2–8 broad, somewhat clavate branches, 195–556  $\mu$  long by 52–111  $\mu$  in diameter, on the termini of which are borne in dense clusters the reproductive organs, and also, in some plants, long slender branched or unbranched setae. Sporangia typically broadly elliptical, often slightly curved; resting on a short, collar-like, truncated basal attenuation; varying from 63–169  $\mu$  in length, majority 88–100  $\mu$  (average 97  $\mu$ ) by 34–63  $\mu$  in diameter, majority 42–52  $\mu$  (average 50  $\mu$ ), usually maintaining a ratio of length to width of 1.3–2.3:1; zoospores spherical, posteriorly uniloculate, 10  $\mu$  in diameter. Resting spores nearly spherical, oval, or somewhat elongate, basally truncate, 39–52  $\mu$  in length by 36–49  $\mu$  in diameter (average  $46 \times 39.6 \mu$ ).

*BLASTOCLADIA GLOMERATA*, sp. n. \*. *Planta omnis, saeptis sterilibus et radicibus exclusis, altitudine 693–920  $\mu$ , moenia solida et levia crassitudine ad 10.4  $\mu$ ; cella solida, basi lato maxime, longitudine 312–364  $\mu$  et per medium 104–162  $\mu$ , raro irramosa, proferens plerumque a duobus ad sex ramos clavae similis, longos 195–556  $\mu$  et latos 52–111  $\mu$ , quorum in terminis et genitalia in corymbis densis lata sunt et in plantis nonnullis saetae aut ramosae aut*

\* I am indebted to Prof. J. B. Stearns for Latin descriptions of this species as well as those of *Myzocyttium zoophorum* and *Pythium perigynosum*.

irramosae. Sporangia plerumque elliptica et saepe curvata minime, in basi brevi et torqui simili posita; longitudine 63–169  $\mu$  (maior pars 88–100  $\mu$ , media 97  $\mu$ ), per medium 34–63  $\mu$  (maior pars 42–52  $\mu$ , media 50  $\mu$ ); zoospores sphaerica, una cilia, 10  $\mu$  per medium. Spermata quiescentia aut prope sphaerica aut ovata aut aliquantum longa, longitudine 39–52  $\mu$ , per medium 36–49  $\mu$  (media  $46 \times 39.6 \mu$ ).

*Blastocladia glomerata* (Pl. 20, figs. 4, 9) appears to be distinct from *B. Pringsheimii*, which from the character of the resting spore it most nearly resembles, in the general shape of the thallus and in the shape of the sporangia. The different aspect of the plant body is brought about in the main by the

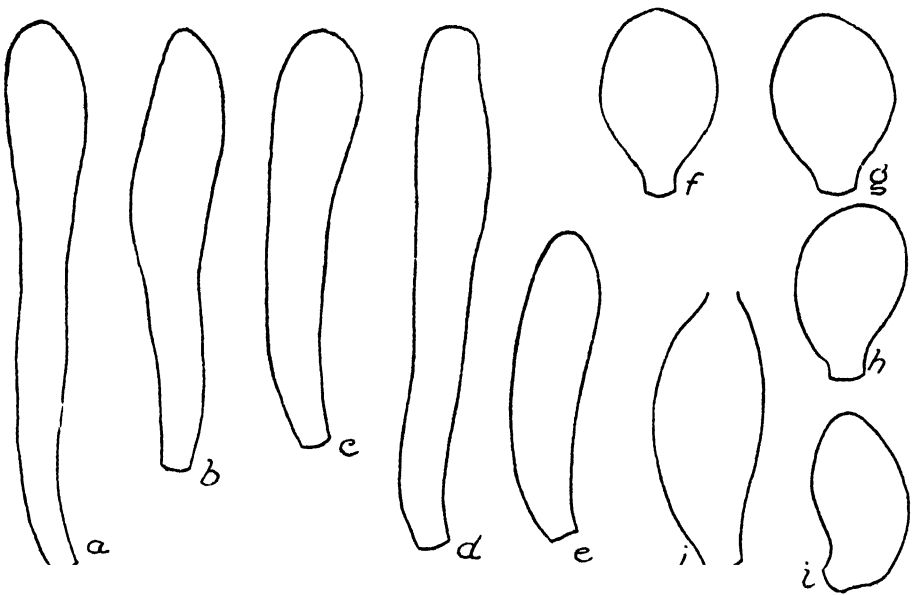


FIG. 5.

a–d. Outline of shapes of sporangia of *Blastocladia Pringsheimii*.

e. Shortest sporangium found of *B. Pringsheimii*; non-typical.

f–j. Outlines of sporangia of *B. glomerata*, sp. n. Fig. j is longest found; non-typical.

(All  $\times 250$ .)

formation of a stout, often strongly tapering, basal cell, from which arise broad branches of considerable length terminated by dense clusters of sporangia. The shape of the sporangia, however, offers the most fundamental difference between the two species, as shown in the outlines of these structures in fig. 5. This distinctiveness is further emphasized when the ratios of length to width of the sporangia of the two are compared. In *B. Pringsheimii* (from plants shown in Pl. 20, fig. 5) this was found to be usually 6.4–8:1, while in *B. glomerata* it was 1.3–2.3:1,

Certain forms figured by Lund (1934, fig. 18, b) and discussed under *B. Pringsheimii* undoubtedly may be referred to *B. glomerata*.

44. *BLASTOCLADIA GLOBOSA* Kanouse. Saprophytic on fruit of apple, Site 3, September to December 1932.

What I interpret as this species forms minute white pustules on the surface of the fruit. The basal cell is nearly spherical, often strongly lobed, up to  $200\mu$  in diameter, and terminates a very short cylindrical stalk about  $60\mu$  in diameter, from the lower part of which the hold-fast system arises. The wall is stout, attaining a thickness of  $10\mu$  in some plants, and is easily fragmented—so easily, in fact, that, as in the preceding species, it is difficult to obtain whole specimens. The cylindrical sporangia varied from  $120$ – $160\mu$  in length by  $25$ – $35\mu$  in diameter. The resting spores, which were like those of *B. Pringsheimii* and *B. glomerata*, were  $30$ – $60\mu$  in length by  $40\mu$  in diameter. No setae nor evidences of the antheridial filaments described by Kanouse (1927) were observed.

45. *BLASTOCLADIA PROLIFFRA* Minden. Saprophytic on twigs of *Fraxinus* sp., Coe Fen, Cambridge, 11 October 1932.

In its general appearance (Pl. 20, fig. 13) *B. proliifera* resembled the common *B. Pringsheimii*. The narrow, cylindrical basal cell varied from  $312$ – $468\mu$  in length by  $13$ – $31\mu$  in diameter, and gave rise at its base to the hold-fast system. The distal portion of the basal cell was strongly expanded, lobed, or more often unlobed,  $47$ – $374\mu$  in diameter, and bore the sessile sporangia and setae. The sporangia were cylindrical,  $73$ – $143\mu$  long by  $13$ – $21\mu$  in diameter and the zoospores posteriorly uniloculate, spherical, and  $5.2\mu$  in diameter. Internal proliferation of the sporangia was frequent and very evident (Pl. 20, fig. 3). The numerous sterile setae were branched or unbranched and up to  $260\mu$  in length. No resting spores were found nor were they described by Minden.

This species differs in one important particular from *B. Pringsheimii*. After discharge of the zoospores internal proliferation of the sporangium occurs in much the same manner as in a species of *Saprolegnia*. Particular care was taken to make sure that this proliferation actually took place and that it was not due to an optical effect produced by superimposed sporangia.

In a number of instances, small specimens of *Blastocladia* were found in company with larger forms. The sporangia were  $70$ – $105\mu$  long by  $10\mu$  in diameter. The basal cell was often extremely long, sometimes appeared jointed, and was  $10$ – $20\mu$  in diameter expanding to  $20$ – $30\mu$  at the tip.

## MONOBLEPHARIDALES.

46. *GONAPODYA PROLIFERA* (Cornu) Fischer. Saprophytic on twigs of *Aesculus* sp., Site 2, August to December 1932; twigs of *Quercus* sp., Site 5, 20 September 1932; twigs of *Quercus* sp., Kew Gardens, 1 November 1932.

An exceedingly common inhabitant of twigs in most fresh-water habitats (Pl. 20, fig. 1).

47. *GONAPODYA POLYMORPHA* Thaxter. Saprophytic on twigs of *Quercus* sp., Kew Gardens, 1 November 1932.

The sporangia (Pl. 20, fig. 8) are ovate rather than siliquaeform as in the preceding species, and the whole plant more delicate.

48. *MONOBLEPHARIS MACRANDRA* (Lagerh.) Woronin. Saprophytic on twigs of *Aesculus* sp., Site 2, August to December 1932; twigs of *Fraxinus* sp., Barton Mills, Suffolk, 14 November 1932.

This is the commonest species of *Monoblepharis* in the vicinity of Cambridge and may be collected at any time of the year.

49. *MONOBLEPHARIS MACRANDRA* var. *LAEVIS* Sparrow. Saprophytic on a twig of *Aesculus* sp., Site 2, 24 December 1932.

This variety, characterized by having smooth-walled instead of bullate-walled oospores was collected only once. It was also found on ash twigs from a small pool in Kongelund, Amager, Denmark, in August 1933.

50. *MONOBLEPHARIS SPHAERICA* Cornu. Saprophytic on twigs (of *Aesculus*?), Site 2, 24 December 1932.

Collected only once.

51. *MONOBLEPHARIS OVIGERA* Lagerh. Saprophytic on hemp seed 'bait' in a gross culture from Site 5, 20 September 1932; saprophytic on fruit of apple, tap water, the Botany School, Cambridge, 30 November 1932; twig, Kew Gardens, 1 February 1933.

## LEPTOMITALES.

52. *RHIPIDIUM EUROPAEUM* (Cornu) Minden. Saprophytic on fruits of apple, twigs of *Fraxinus* sp., Sites 2, 3, throughout the year.

The arborescent thallus of both this and the following species consists of a basal cell often very similar to that of *Blastocladia*, but more gnarled and contorted, on which are placed the sporangia and sex organs, and a hold-fast system. The sporangia are ovate, or occasionally narrowly obpyriform, and are formed on branches of varying length which are separated from the platform of the basal cell by a narrow hyaline plug or pseudosepta. In exceptionally long filaments constrictions and false septations may occur. The

sex organs are generally borne on shorter hyphae, which also arise from the distal face of the basal cell. The oogonium is spherical or occasionally obpyriform and about  $33\mu$  in diameter; the single, basally applied, clavate antheridium, which is borne on a tenuous, somewhat contorted, often branching filament, arises from some nearby hypha and is about  $10\text{--}13\mu$  in diameter (Pl. 20, fig. 10). After fertilization the contents of the oogonium become transformed into a spherical or obpyriform oospore, the outer thickened golden wall of which is raised in a series of very pronounced, anastomosing ridges. These oospores, which nearly fill the oogonium, vary from  $31\text{--}33\mu$  in diameter; occasional elongate ones,  $39\text{--}41.6\mu$  long by  $26\text{--}31\mu$  in diameter, are also formed.

Discoid or peltate thalli similar to those figured by certain other observers of this species were frequently found (Pl. 20, fig. 6), particularly on hard varieties of apples, on which they formed very minute pustules similar to those of *Blastocladia globosa*.

Lund's (1934) resumption of the binomial *Rhipidium continuum* Cornu for this species has much in its favour.

53. *RHIPIDIUM AMERICANUM* Thaxter. Saprophytic on twigs of *Quercus* sp., Site 5, 20 September 1932.

While some of the material collected in the vicinity of Cambridge may possibly be referable to this species, the tenacious debris surrounding the sex organs made it impossible to determine the origin of the antheridium. This character alone seems to distinguish the species from *R. europaeum*. In the material from Haslemere the androgynous antheridium is produced at the tip of a short, strongly arched stalk, which ordinarily arises immediately beneath the pseudo-septa of the oogonium (Pl. 20, fig. 2). There were no significant differences in the sizes of the parts or in the general appearance of the plant when compared with *R. europaeum*.

A few specimens of what may be *Rhipidium parthenosporum* Kanouse were found on twigs collected at Site 2, 24 December 1932. On the same branches of the narrowly cylindrical thallus which bore ellipsoid sporangia, there were observed several spherical, somewhat thick-walled bodies. While the walls were noticeably thicker than those of the sporangia, no 'cellular' disposition of the protoplasm such as described by Kanouse (1927) was noted.

54. *SAPROMYCES REINSCHII* (Reinsch) Fritsch. Saprophytic on twigs of *Quercus*, Site 5, 20 September 1932.

A limited amount of this material was found on twigs in company with a species of *Achlya*. From the narrow basal cell, presumably anchored to the substratum by hold-fasts, arose the long slender hyphae,  $10\text{--}13\mu$  in diameter. These were constricted by refractive pseudo-septa at intervals of  $250\text{--}875\mu$ . Only sex organs were found. The smooth-walled colourless oogonia, which were terminally or laterally disposed on the hyphae, were obpyriform,  $31\text{--}42\mu$



in height by  $23\text{--}26\ \mu$  in greatest diameter, and were borne on short pedicels formed by the narrow pseudo-septa immediately beneath them. The extensive dichinous antheridial branches were generally about  $5\ \mu$  in diameter and were often twisted and contorted. On the tips of each of these was a clavate antheridium,  $26\ \mu$  long by  $13\ \mu$  in diameter, which usually twisted around and made broad contact around a conspicuous fertilization tube with the apex of the oogonium (Pl. 20, fig. 11). The oospores, which did not fill the oogonium, were spherical,  $23\text{--}26\ \mu$  in diameter, and possessed a thick brownish wall, the outer surface of which was raised in a series of irregular ridges.

Through the kindness of Dr. B. Barnes I have examined an abundance of material of this species in both sexual and non-sexual stages, which was found by him on submerged oak twigs.

### SAPROLEGNIALES.

55. *SAPROLEGNIA ASTEROPHORA* de Bary. Saprophytic on hemp-seed bait, in soil culture from heath near Mildenhall, Suffolk, 16 November 1932.

56. *ACHLYA COLORATA* Prings. Saprophytic on grass stem, Site 5, 20 September 1932.

57. *DICTYUCHUS MONOSPORUS* Leitgeb. Saprophytic on twigs, hemp seed, all sites in the vicinity of Cambridge throughout the year; twig, Kew Gardens, 1 November 1932; twig of *Fraxinus*, Barton Mills, Suffolk, 16 November 1932.

*Dictyuchus* seems to be the commonest water mould in the vicinity of Cambridge. The parthenogenetic strain reported by Couch (1926) was frequently found.

58. *THRAUSTOTHECA CLAVATA* (de Bary) Humphrey. Saprophytic on hemp seed in soil culture, York, 8 September 1932.

59. *APHANOMYCOPSIS BACILLARIACEARUM* Scherffel. Parasitic on *Synedra* sp., Site 1, 8 March 1933.

60. *ECTROGELLA MONOSTOMA* Scherffel. Parasitic on *Synedra* sp., Site 1, 8 March 1933 (fig. 4, p).

61. *APHANOMYCES PARASITICUS* Coker. Parasitic in hyphae of *Dictyuchus monosporus*, Barton Mills, Suffolk, 16 November 1932.

### ANCYLISTALES.

62. *MYZOCYTIUM ZOOPHORUM*, sp. n. Parasitic in rotifers and rotifer eggs, Site 4, 3 March 1933.

Mycelium intramatrical, at first tube-like and non-septate, later becoming

septate, the segments  $5-17\ \mu$  in diameter, of variable length, rarely branched, constricted or unconstricted; septations narrow and inconspicuous. Sporangia consisting of irregular, sac-like, often lobed portions of the thallus, each of which produces a single, generally short discharge tube which penetrates the host wall; zoospores laterally biciliate,  $10-11\ \mu \times 6-7\ \mu$ , partially or wholly delimited within the sporangium, discharged through the evacuation tube and forming an amorphous subspherical mass at the tip of the tube, which quickly becomes separated into a number of irregular segments, the immature zoospores, which complete their development at the mouth of the tube. Sexual reproduction by conjugation of adjacent segments of the thallus, the content of one passing into the other through a pore formed in the wall separating them; oospore spherical, thick-walled,  $12-15\ \mu$  in diameter, with a single reserve globule, lying loosely in the oogonium; germination not observed.

*MYZOCYTIUM ZOOPHTHORUM*, sp. n.

Mycelium intramaticale, primum tubulo simile et non divisum, postea divisum cum segmentis  $5-17\ \mu$  per medium, longitudine variis, raro ramosis, contractis aut non contractis; divisiones angustae et obscurae. Sporangia sunt inaequalium thalli partium sacco similium, quarum, singulae partes tubulos breves et moenia hospitis penetrantes perferunt; zoospora cum duobus a latere ciliis  $10-11 \times 6-7\ \mu$ , aut partim aut omnino in sporangio describatis, per tubulum prolata et in extremo tubulo informem subsphaericam molem formantia quae cito in inaequalibus segmentis, scilicet immaturis zoosporis, se dividit. Procreatio est sexualis, segmentis finitimis thalli coeuntibus; ita fit ut quae in uno segmento sunt in alterum segmentum per foramen muri inter duo segmenta eant. Oosporae sphaerae, cum muris crassis,  $12-15\ \mu$  per medium, uno globulo subsidiario in oogonio solute iacente; germinatio non observata.

*M. zoophthorum* was a virulent parasite of both active animals and their eggs. Not only were there found many dead infected rotifers (Pl. 19, figs. 5-7), but in several instances living, actively moving animals were observed, with encysted zoospores attached to their shells (Pl. 19, figs. 3, 4) and even rudiments of the mycelium within them (Pl. 19, figs. 1, 2).

The zoospore after becoming attached in some unknown manner, perhaps by a mucilagenous secretion, to the outer wall of the animal, forms a rather stout cylindrical tube which bores through the shell (Pl. 19, fig. 3) and produces within a small spherical structure (Pl. 19, fig. 4). The latter enlarges as the protoplasm of the cystospore passes into it, and there is ultimately formed a curved, unbranched tube (Pl. 19, fig. 2) which elongates and becomes the thallus. The latter, while often strongly lobed, rarely seemed to be distinctly branched. Several spores may attack a single animal and produce thalli within it. Extensive infection of the eggs was also noted (Pl. 19, figs. 8, 9). In these, the thallus often remained more isodiametric than in the animals and showed a tendency to form narrow branch-like lobes (Pl. 19, fig. 9). In the

discharge of the spores, no evidences of a vesicle could be observed, save perhaps at the initiation of the process, when the first few bodies ejected formed a subspherical compact mass (Pl. 19, figs. 11–13). The majority of the swarmers emerged from the tube individually (Pl. 19, fig. 14), and quickly formed a writhing cluster at the orifice during the brief period of formation of their cilia (Pl. 19, fig. 8).

I am in some doubt as to the generic disposition of this fungus. In the link-like, generally unbranched nature of its thallus it resembles a species of *Myzocyttium*, particularly *M. vermicolum* Zopf. It differs from the latter, however, in the longer, more tubular, often contorted segments which approximate in this character to those of a species of *Lagenidium*—for example, *L. pygmaeum* Zopf. Indeed, in certain features the rotifer parasite resembles both these genera. Thus, in the typical unbranched thallus found in the active stages of the host and in the unspecialized antheridial cell (Pl. 19, fig. 6), it resembles *Myzocyttium*, whereas in the eggs of the host a slender, more tubular, occasionally branched, *Lagenidium*-like body is formed. Unlike *Lagenidium*, however, no specialized antheridial branch has ever been observed, and for this reason it is considered a species of *Myzocyttium*.

This same parasite was found in rotifers, and their eggs, collected in a small pond among the dunes in northernmost Jutland, Denmark, in July 1933.

Several other fungi, probably members of the Ancylistales, were found, but only incomplete notes on their life-histories were obtained. The first of these (fig. 4, *g*), which was parasitic in *Synedra* (?) sp., collected at Site 1 in September 1932, consisted of a linear series of elliptical structures, each 20–22  $\mu$  long by 18–20  $\mu$  in diameter, which were connected to each other by narrowly cylindrical, very refractive isthmuses. No reproductive activity was observed. The fungus appears to be a species of *Myzocyttium* with very elongated septations. A second form was found in the resting cysts of *Euglena* collected at Site 4 on 3 March 1933. The stout, branched, twisted, and irregular mycelium (Pl. 17, figs. 14, 15), 3–8  $\mu$  in diameter, while at first entirely intramatrical, ultimately bored through the walls of the host and formed a limited extramatrical system. No evidences of sporangial formation could be found. However, certain elliptical thick-walled resting spores (Pl. 17, fig. 13),  $10 \times 7 \mu$ , at first considered to be those of *Entophlyctis apiculata*, were found. Under high magnification these spores were observed to be intimately associated with empty hyphae. It is probable that the organism is a small species of *Lagenidium*. To the same genus may possibly be referred the immature thallus found, in association with *Achlya*, *Aphanomyces*, and *Rhizophidium*, on the nematode cadaver (Pl. 19, fig. 16, *a*). Attention might also be called to the remarks concerning the affinities of the fungus doubtfully termed *Pleotrachelus Petersenii* in this paper.

## PYTHIALES.

63. *PYTHIUM TENUE* Gobi. Parasitic in *Vaucheria* sp., Streighton, Cambs., 18 September 1932; Site 1, 12 September 1932.

64. *PYTHIUM PERIGYNOSUM*, sp. n. Saprophytic on hemp-seed 'bait' in debris from Site 5, 20 September 1932.

Mycelium composed of relatively straight main hyphae,  $5.2\mu$  or more in diameter, and numerous straight, or more often irregular or tortuous, narrow lateral branches; appressoria rare, usually entirely lacking. Sporangia (in pure water cultures) consisting of undifferentiated portions of the mycelium, separated from the remainder by cross-walls; evacuation tube of variable length with a somewhat distended apex. Zoospores variable in number, up to 60 observed in a single vesicle; about  $13\mu$  in length by  $8\mu$  in diameter, ultimately forming a cystospore  $10\mu$  in diameter, which upon germination produces a germ tube about  $3\mu$  in diameter. Oogonia (on maize agar and hemp seed in water culture) generally terminal on the irregular lateral branches, occasionally intercalary, when terminal usually apically papillate; with a smooth wall approximately  $.8\mu$  in thickness; spherical or subspherical,  $13-20.8\mu$  in diameter, the majority  $15.6\mu$ ; the delimiting septum (or septa) only slightly exerted beyond the contour of the structure. Antheridia generally of the 'crook-neck' type,  $8-13\mu$  long by  $5-7.8\mu$  broad in the more distal portion, the tip of the latter truncate and making relatively broad contact with the oogonium; fertilization tube about  $2\mu$  in diameter; usually 1-2 androgynous, autonomous, borne on a somewhat curved branch which arises in the vicinity of the oogonium, occasionally 3-5 borne on the tips of branches which may usually be traced to the main hypha, which also gave rise to the oogonial branch. Oospores smooth-walled, the wall about  $.8-1.4\mu$  thick, lying loosely in the oogonium, although occasionally nearly filling it;  $12-15\mu$  in diameter, majority  $13\mu$ ; with a reserve globule about  $8\mu$  in diameter and a smaller spherical or elliptical structure in the somewhat golden content; germination not observed.

*PYTHIUM PERIGYNOSUM*, sp. n.

Mycelium hypharum comparte rectarum, per medium aut  $5.2\mu$  aut plus, et multorum aut rectorum, aut saepius inaequalium ramorum angustiorum; appressoria rara, plerumque non sunt: Sporangia mycelii partium a reliquo muris separatarum; tubulus varia longitudine cum apice allquantum distento. Zoospora varia numero, ad 60 in una vesicula observata, circa  $13\mu$  long,  $8\mu$  diameter, cystosporam demum  $10\mu$  dia. formantia, quae germinans tubulum spermatorum circa  $13\mu$  dia. profert. Oogonia plerumque terminalia in inaequalibus a latere ramis, saepe in apice papillata, muro levi circa  $.8\mu$  crassitudine, sphaerica aut subsphaerica,  $13-20.8\mu$  dia. (magna pars  $15.6\mu$ ) cum saeptis paulo modo ex forma herbae eminentibus. Antheridia

plerumque generis Anglice cervicis torti appellati, long. 8–13  $\mu$ , lat. 5–7·8  $\mu$  in parte expansa; acumen huius partis praecisum et latius oogonium tangens; tubulus fecundus circa 2  $\mu$  dia.; plerumque antheridia aut 1 aut 2 androgyna, autonoma, in aliquantum curvato ramo lati, qui prope oogonio oritur, sed per occasionem antheridia a 3 ad 5 in extremis ramis lati. Oosporae levibus muris; muris 8–1·4  $\mu$  crassitudine; in oogonio laxae iacentes sed per occasionem oogonium prope implentes; 12–15  $\mu$  dia. (magna pars 13  $\mu$ ); cum globulo subsidiario circa 8  $\mu$  dia. et minore aut sphaerica aut elliptica mole; germinatio non observata.

The present fungus (fig. 7, *l-t*) appears to be closely allied to *Pythium tenue* Gobi, *P. angustatum* Sparrow, and *P. dissotocum* Drechsler. While similar to the first-named in the size of its parts, the narrow wall of the oospore and particularly in the androgynous origin of the usually single antheridium, *P. perigynosum* differs in the generally longer antheridial branches, the broader and more abruptly crooked antheridium, and in the presence in the latter structure of a definite delimiting septum—the lack of which in *P. tenue* has been attested to by both Gobi (1899) and Matthews (1931). Further, the British fungus is easily cultivated on artificial media as contrasted with the material from *Vaucheria* described by Matthews.

*Pythium perigynosum* resembles *P. angustatum* in the narrowness of its oospore wall. However, differences in the size of the sexual apparatus, and particularly in the antheridia, are evident. The most important of these appears to be the fact that in *P. angustatum* a greater number of antheridia are applied to an oogonium, and that these are typically diclinous in origin.

While the absence of figures of *Pythium dissotocum* (Drechsler, 1930) makes comparison difficult, from the rather complete description given many similarities with the present fungus are apparent. No great differences in the sizes of the parts separate them, although the majority of the oogonia and oospores of Drechsler's species are somewhat larger (17–25  $\mu$ , 15–21  $\mu$ , compared with 15·6  $\mu$ , 13  $\mu$ ). In the origin, shape, and number of the antheridia of *P. dissotocum* further resemblances are found. However, no mention is made of the arching habit of the antheridial stalk, so typical of the present material; nor has the latter exhibited any tendency for the occasional formation of swollen dactyloid elements connected with the sporangial apparatus. Other differences between the two might be noted. Of these, the frequent formation in *P. dissotocum* of oogonial cross-walls at some distance (up to 8  $\mu$ ) along the concomitant hypha, the statement that the oospores '... usually very largely though not completely ...' fill the oogonium, the somewhat thicker oospore wall (average 1·5  $\mu$ ), and, to a lesser degree, the lack of a terminal papilla on the oogonium appear most evident.

65. ZOOPHAGUS INSIDIANS Somm. Parasitic on rotifers, Site 2, 9 August 1932; Streighton, Cambs., 18 September 1932; Coe Fen, Cambridge, 26 November 1932; Kew Gardens, 1 February 1933.

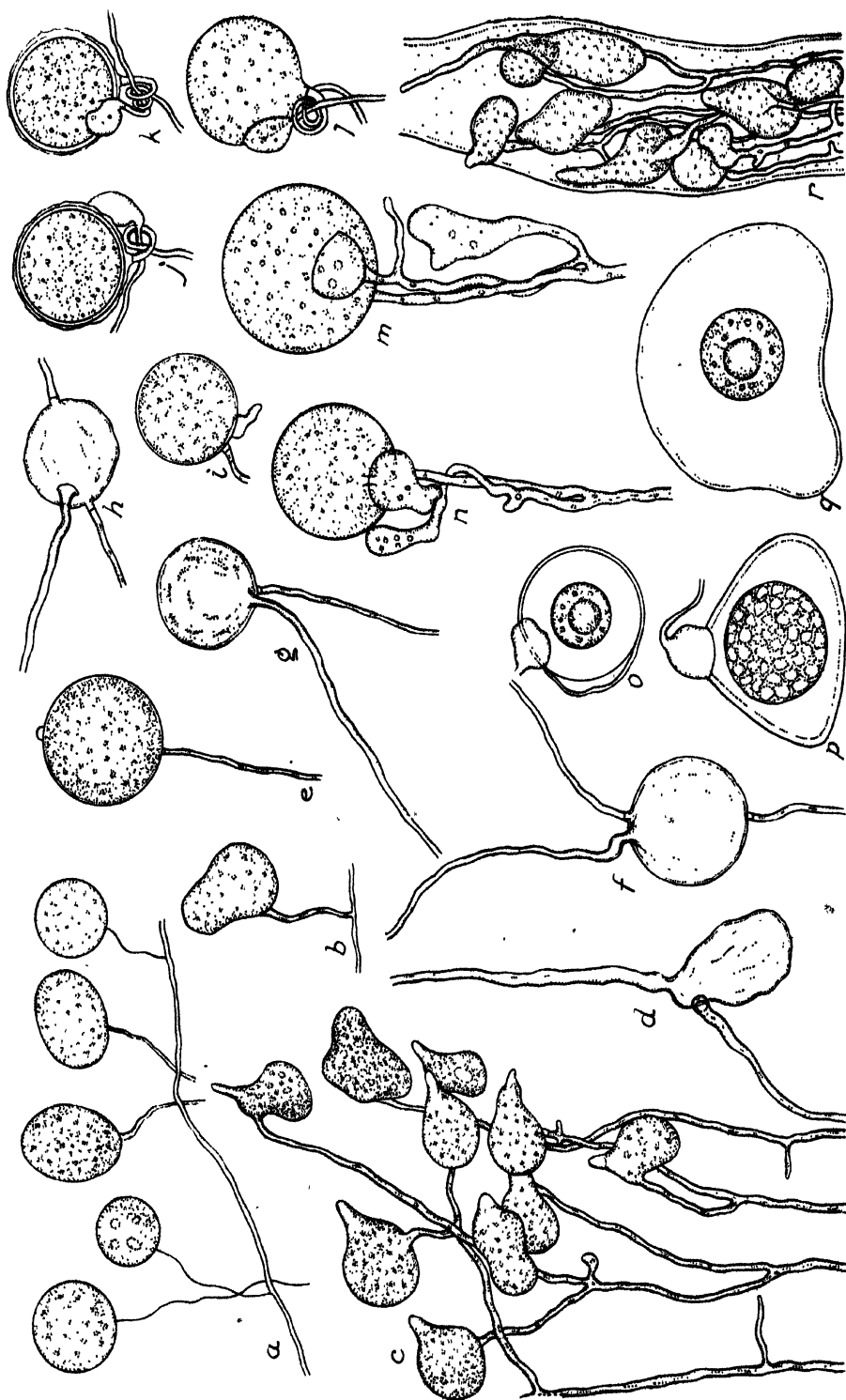


Fig. 6.

## EXPLANATION OF FIG. 6.

*Pythiogeton* spp.

- a, b. Group of sporangia from Haslemere illustrating variations in shape found. The large majority were spherical.  $\times 348$ .
- c. Group of immature sporangia of *P. utriforme* (?) type from Coe Fen, Cambridge.  $\times 348$ .
- d. Discharged sporangium from same material.  $\times 348$ .
- e. Type of sporangium associated with sex organs shown in figs. j-l.  $\times 348$ .
- f-h. Empty sporangia from same material showing long discharge tube generally formed near point of attachment of sporangium to hypha.  $\times 348$ .
- i. Sporangium from same material showing beginning of formation of basal discharge tube.  $\times 348$ .
- j, k. Sex organs associated with sporangia of figs. e-i, showing oogonial stalk encircling antheridial filament. Oospores probably not mature.  $\times 560$ .
- l. Earlier stage in development of sex organs.  $\times 560$ .
- m, n. Sex organs found in material from Site 2.  $\times 600$ .
- o. Oospore showing oogonial wall distinct from that of spore.  $\times 600$ .
- p. Oospore of unusual shape and disposition of contents.  $\times 600$ .
- q. Large oospore of unusual shape, but with contents typically disposed.  $\times 600$ .
- r. Sporangia of *P. utriforme*-type in hypha of *Achlya*.  $\times 348$ .

66. PYTHIOMORPHA GONAPODYIDES Petersen. Common in the vicinity of Cambridge throughout the year on decaying twigs.

67. PYTHIOGETON spp. Saprophytic on decaying twigs throughout the year in the vicinity of Cambridge.

In view of the present uncertain status of the hitherto established species of *Pythiogeton*, brought about in the main by Drechsler's recent study of a form termed by him *P. autossyrum* (1932), it would seem best for the present merely to give an account of the various types of fungi evidently belonging to this genus which were found in some abundance in the course of this investigation. Further work involving an extensive cultural study of the forms found in the field will evidently be necessary before any lines of specific demarcation can be drawn with certainty. It might be mentioned here that I was uniformly unsuccessful in my attempts to obtain these fungi in artificial culture.

Members of the genus abound in old gross water cultures of twigs, where they occur either at the base of the pustules formed by larger aquatic moulds or more especially in the soft tissue at the broken ends. Numerous collections were made in the vicinity of Cambridge at all times of the year, particularly at Sites 2 and 3, where they were also found on fruits of apple. Material was also obtained on twigs of *Fraxinus* from Coe Fen, Cambridge, Barton Mills, Suffolk, and Site 5.

As representative of the main sporangial types found, of which there were many variations, fig. 6, a-i, might be examined. The first of these (fig. 6, c), from Coe Fen, in the shape and position of its sporangia bears a marked resemblance to *P. utriforme* Minden. The narrow, irregularly branching

hyphae produce at their termini broadly sac-like or bursiform sporangia. The latter in this material varied from 32–45  $\mu$  in length by 17–30  $\mu$  in greatest diameter, and were borne with their long axes at right angles, or less, to that of the supporting hyphae. In several instances the fungus had invaded the hyphae of larger water moulds (fig. 6, *r*), and there had produced sporangia and sexual organs. There was nothing to suggest that the fungus had parasitized the larger organism, although the ease with which the tips of these intramatrix sporangia had bored through the thick surrounding walls was very suggestive (Pl. 20, fig. 12). Discharged sporangia of the *utriforme*-type frequently possessed a long, somewhat irregular evacuation tube (fig. 6, *d*). Fig. 6, *a*, depicting material collected at Site 5, illustrates another type of sporangium frequently found, which is generally unassociated with sporangia of any other shape. Save for their almost constant terminal position they resemble those doubtfully referred to in a previous paper (1933 *c*) as *P. transversum* Minden and more recently segregated as *P. uniforme* by Lund (1934). The sporogenous structures were in the main spherical, 22–32  $\mu$  in diameter, thin-walled, and borne on exceedingly tenuous hyphae. From the large size of the sporangia when compared with the exceedingly tenuous hyphae, this material resembles *Pythium diacarpum* Butler. A third type, apparently closely allied to the preceding one, is illustrated in fig. 6, *e-i*. This form, found abundantly at Site 2 on twigs, also possessed spherical sporangia, but these were slightly larger than those formed by the Haslemere fungus (40–48  $\mu$  in diameter) and possessed a distinctly thicker wall. As in those of the preceding types, an evacuation tube of considerable length was produced, which in terminal sporangia was often formed in the immediate vicinity of the point of attachment to the hypha.

In this same material there also occurred a large number of intramatrix sex organs, three of which are shown in fig. 6, *j-l*. While every effort was made to trace the mycelial connections of these structures, and to link them up with the sporangia, the tenuous nature of the hyphae made this so extremely difficult to demonstrate that positive proof is lacking. However, from the association of large numbers of both types of structures in the same pustule, from the exact similarity of the hyphae both in size and method of branching, and from the absence in the material of any other Phycomycete, the vegetative system of which even approaches that of the *Pythiogelon*, it seems more than probable that we are dealing with a single organism. The peculiar helicoid involvement of the antheridial filament by that bearing the oogonium, as shown in fig. 6, *j-l*, is strongly suggestive of the situation described by Minden as prevailing in sex organs associated by him with *P. transversum*. In the British material, as in the German, the opposite condition was occasionally found. Further, in both *P. transversum* and the present form the didymous antheridium was applied at or near the base of the terminal oogonium. In the material under discussion it is probable that fully mature oospores were not observed, for in the most advanced stage found (fig. 6, *j, k*) the spherical oospores



were relatively thin-walled, and did not possess the characteristic internal organization usually associated with such bodies. These resting spores were about  $33\ \mu$  in diameter and were surrounded by the thin wrinkled wall of the oogonium. No evidence of the polygonal shape assumed by the oogonium of *P. transversum* was noted.

A somewhat different type of sexual apparatus, probably belonging to a species of this genus was found in a collection from Site 2. Here (fig. 6, *m, n*), the antheridia were clearly androgynous, and while more than one was produced on a branch only one was functional. The slight degree of involvement of the hyphae bearing the two different organs was, for the most part, accomplished by the antheridial filament. In their general features and size of their parts (oogonium  $32\text{--}40\ \mu$  in diameter, antheridium  $15\ \mu$  in diameter), these structures closely resemble the sex organs of *P. utriforme*. However, no sporangial stage was found associated with them.

Mature oospores, similar to those figured by Minden for *P. utriforme* and characterized by the presence of an extremely thick hyaline wall, were found in many collections. Unfortunately, due mainly to the fact that they were practically always formed within the woody substratum, their mycelial connections were always torn away in teasing them out from their matrix, thus precluding the possibility of connecting them absolutely with the sporangia which usually accompanied them. From the almost constant association of the two stages, particularly when both occurred in the filaments of water moulds (Pl. 20, fig. 12), I feel, in spite of the lack of direct proof, that they belong to the same organism. These peculiar resting bodies, unlike any formed by other members of the Pythiaceae, not only in the extreme thickness of the surrounding wall but in the unusual internal organization, often though not always exhibited, were generally elliptical or spherical. Occasional somewhat irregular examples were found (fig. 6, *p, q*).

As has been stated, my observations on the fertilization and maturation of the oospore are inadequate. There probably takes place after fertilization a gradual contraction of the granular protoplasm, which as it retreats is replaced by the hyaline wall material (fig. 7, *a-c*). From observations on the structure of the mature oospore, I am inclined to interpret the outer wall of the hyaline material as the outer wall of the oospore, which is nearly always fused to the scarcely perceptible wall of the oogonium; the very slightly thickened boundary of the small sphere of protoplasm within is considered the inner wall. Confirmation of this concept is to be found in such spores as that shown in fig. 6, *o*, in which the oogonial and oospore walls have become separated. These cases are, however, extremely rare, the usual condition being that of complete fusion of the two. The internal organization of the contents is similar to that found in species of *Pythium*, save that around the periphery of the large reserve globule, and often around the whole content, there may generally be detected numerous smaller droplets which often appear as minute punctations. The presence of many irregular refractive granules rather than the single reserve

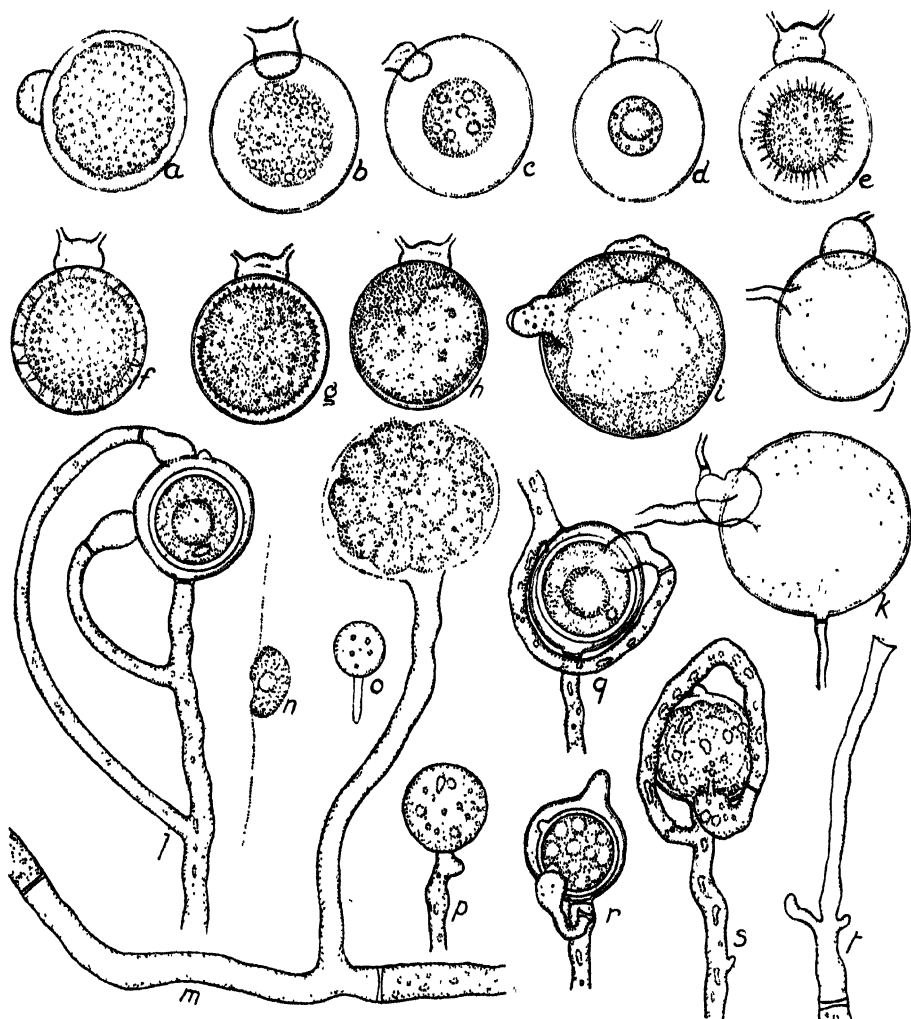


FIG. 7.

- a-c. Three stages in the maturation of the oospore.  $\times 600$ .  
d-h. Successive stages in the germination of an oospore.  $\times 600$ .  
i. Most mature stage obtained in germination of oospore.  $\times 600$ .  
j, k. Two empty oogonia with discharge tubes through which the content of the germinated oospore has evidently emerged.  $\times 600$ .  
l. *Pythium perigynosum*, sp. n. Mature oospore, showing origin and disposition of antheridia.  $\times 780$ .  
m. Formation of zoospores.  $\times 780$ .  
n. Active zoospore.  $\times 780$ .  
o. Germinating cystospore.  $\times 780$ .  
p. Very young stage in development of sex organs showing subspherical terminal oogonium and beneath it the outgrowth which will become the antheridial stalk.  $\times 780$ .  
q, r, s. Showing typical disposition of sex organs. The strongly papillate oogonium in fig. r and papillate oospore are not typical.  $\times 780$ .  
t. Discharged sporangium.  $\times 780$ .

globule, a condition evident in most of Minden's figures of oospores, is not regarded as typical. Such a condition has been frequently noted in a number of oospores (fig. 6, *p*) which, when compared with others in the same mount, were obviously immature.

Practically the whole process of germination of the oospores was observed. A number of these, recovered from old water cultures which had been about seven months in the laboratory, were placed on open slides containing either a film of maize-meal agar, drops of pea broth, or sterile water, and were left in moist chambers overnight at room temperature. The addition of the nutrient materials apparently was needless, for the process about to be described occurred in all the mounts.

The first indication of germination was a slight increase in the amount of the protoplasmic contents and the peculiar appearance of the hyaline wall material. The latter, instead of presenting a uniformly hyaline and refractive aspect, became charged with faint shadowy areas of indefinite shape. Twelve hours after being placed in the moist chambers, the contents had lost the reserve globule, had increased markedly in diameter, and the periphery had become studded with a large number of spine-like protuberances (figs. 7, *d, e*). During the succeeding twenty-four hours the contents expanded further, had become densely granular, and the spines had increased in breadth and had reached the inner wall of the oogonium (fig. 7, *f*). In another twenty-four hours the contents had almost reached the oogonial wall and the spines had again become only short peripheral attenuations (fig. 7, *g*). Within the following twenty-four hour interval the spines had disappeared and the contents occupied practically the whole oogonium (fig. 7, *h*). At this stage the dark granular protoplasm frequently contained large transient vacuoles, and the whole protoplasmic surface appeared covered with minute globules. Many of the spores did not develop further, whereas others formed within the next few days a discharge tube of variable length (fig. 7, *i*). Unfortunately, no means employed would induce the ejection of the contents at an appropriate moment, although such action must have occurred during my absence, for one week after the mounts were prepared several empty germinated spores were found (fig. 7, *j, k*). The contents had evidently been discharged through the tube, probably in a manner similar to that of the sporangium.

While some differences were noted in the time necessary to accomplish the germination of the oospore, the larger ones taking longer than the smaller, the sequence of events appeared always to be the same.

The curious production of 'spines' during the germination process is indeed peculiar, and, so far as I am aware, has thus far not been reported in other members of the family. The true nature of these structures must necessarily await further, cytological investigation, although I am inclined to regard them as essentially vacuolate in character.

## DISCUSSION.

Since matters of specific morphological and biological import, having to do with particular fungi, were taken up in the body of the paper, a more general consideration of certain other points of interest brought out by this study might be briefly discussed.

Certain features concerning the occurrence and collection of these organisms seem worthy of mention. The collections from Sites 1 and 5 are of particular interest, since they illustrate two important points in the routine process of collection. If Table I be examined it will be seen that seventeen different fungi, many of them 'rare' and interesting forms, including two new genera and four new species, were obtained from Site 1. This number by no means represents the total Phycomycetous flora of that locality, since with more collections the number could no doubt be easily doubled. It does show, however, that, in studying these fungi, it is not necessary to cover a large territory in a search for interesting forms. Rather, a single site plentifully supplied with appropriate substrata will suffice. It would have been of interest to note whether the flora of such a site varied over long periods of time.

In Site 5 there is illustrated another, perhaps even more significant, point. It will be recalled that only a single collection was made from this pond, and that the material was distributed in small quantities in shallow dishes and moistened or barely covered with sterile water. Each dish could then be considered a miniature representative of the site and the same collecting technique applied as to the original pond itself. While the probability of finding a large number of fungi would be greatly reduced by this method, yet representatives would be obtained which would give us at least a fragmentary picture of the mycologic flora of the site. Indeed, a perusal of Table I will show that nearly as many different fungi (15) were obtained at Site 5 in one collection as at Site 1 in eleven collections (17). By an application of this type of technique a few interested workers can undoubtedly extend immeasurably our meagre knowledge of the geographic range of the aquatic Phycomycetes. To put this idea to the test, I was fortunate in getting the co-operation of Mr. E. F. Warburg of Trinity College, Cambridge, Mr. B. d'Oliveira of the Instituto Superior de Agronomia of Lisbon, Mr. C. G. Hansford, pathologist, of Uganda, and Mr. J. C. Hopkins, pathologist, of Southern Rhodesia, to all of whom I extend thanks. Mr. Warburg brought back from Tangier a small tin of moist vegetable debris from an aquatic site; the Portuguese collection consisted of forest top soil, that from Uganda two small tins of moist clay from Lake Kioga at Bugando, and the Rhodesian, vegetable trash and soil. All save the Rhodesian material, when properly treated, yielded Phycomycetous fungi. Needless to say, this debris was thoroughly sterilized before discarding. Although the results of these trials are admittedly meagre, yet they do illustrate the feasibility of developing this type of investigation.

Finally, it might be remarked that, while new or hitherto uncollected species are inevitably found in the course of such an investigation as the present one, a general consideration of the aquatic mycologic flora observed in Great Britain, as represented at Cambridge, when compared with similar sites in the eastern United States reveals them to be very much the same, if not identical.

It is a genuine pleasure at this time to express my sincerest thanks to my colleagues for their many kindnesses to me during my stay in England. Particularly am I indebted to Dr. E. J. Butler, F.R.S., for his placing at my disposal the excellent facilities of the Imperial Mycological Institute, and for his helpful advice and enthusiasm, and for giving of his comprehensive knowledge of the habits of these peculiar organisms. To Mr. John Ramsbottom, Keeper of Botany of the British Museum, I am—in common with many other foreign botanists—grateful, not only for making the resources of that institution readily available, but for so successfully and genially providing, what is perhaps to the visitor of even greater import, the opportunity of discussing with his colleagues subjects of mutual interest. Above all, heartiest thanks are due to Mr. F. T. Brooks, F.R.S., who, during the writer's stay at the Botany School, by his stimulating advice, sound criticism, and generous giving of his time, greatly facilitated the progress of this investigation.

This work was done during the tenure of a National Research Council Fellowship in the Biological Sciences.

Dartmouth College, Hanover, N.H.

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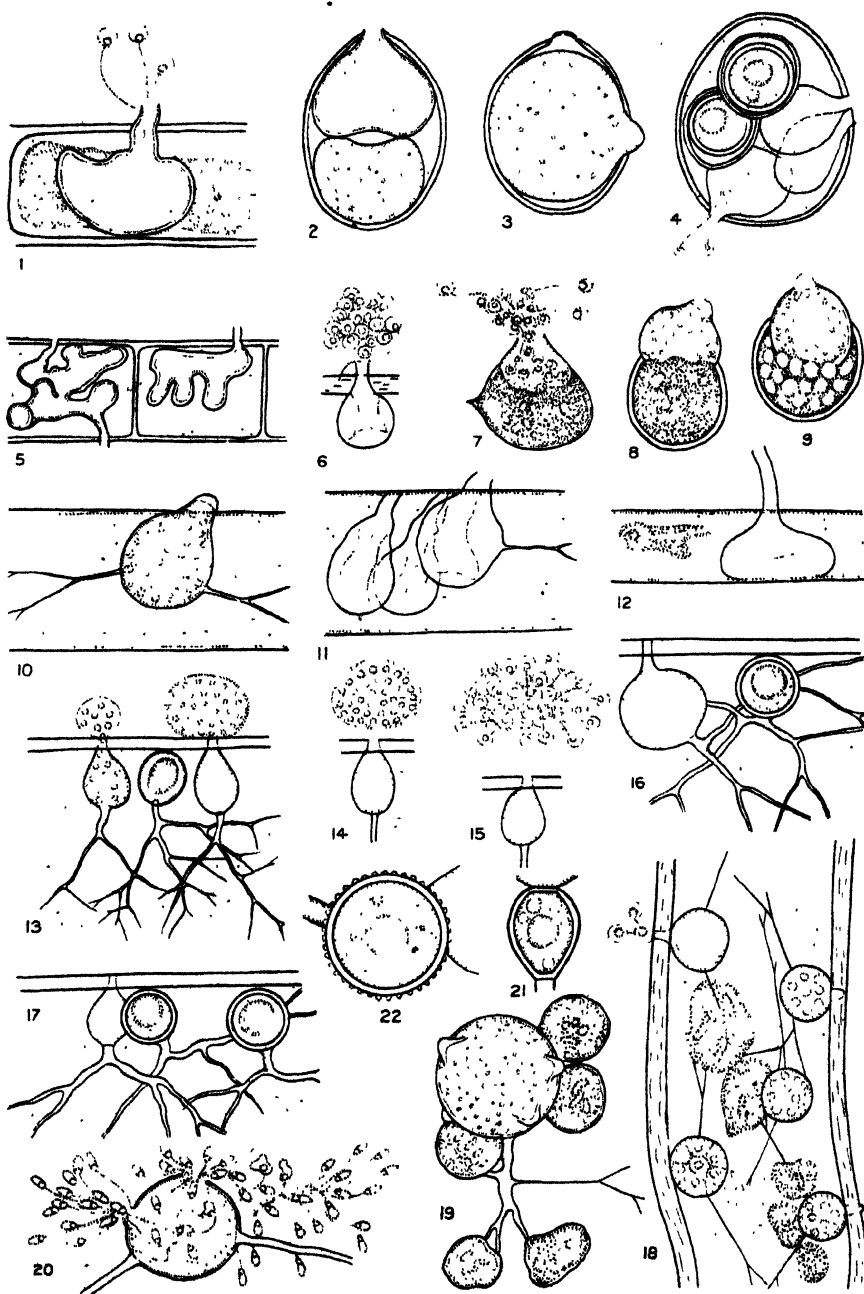
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#### EXPLANATION OF THE PLATES.

All figures were drawn with the aid of the camera-lucida from living material, unless otherwise stated. The approximate magnifications are given.

#### PLATE 14.

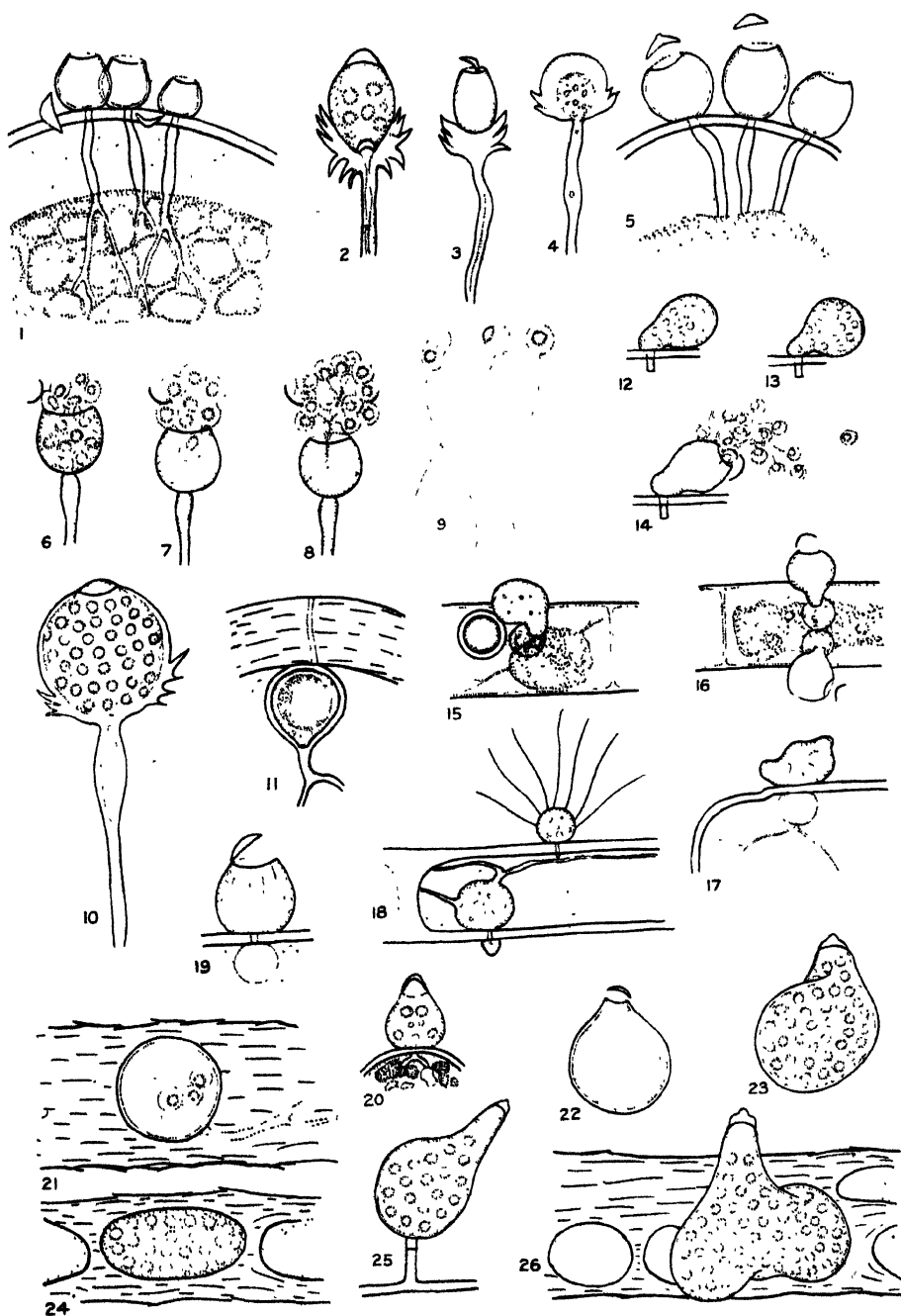
- Fig. 1. Discharging sporangium of *Olpidium endogenum* on *Zygnema*. × 530.
- Figs. 2–3. Immature and discharged sporangia of *Olpidium gregarium* in eggs of rotifer. × 530.
- Fig. 4. Resting spores and empty sporangia; last of zoospores emerging from one sporangium. × 530.
- Fig. 5. Empty sporangia of (?) *Pleotrichus Petersenii* in *Zygnema*. × 530.
- Fig. 6. Discharged sporangium of *Olpidium entophyllum* in *Cladophora*. × 630.



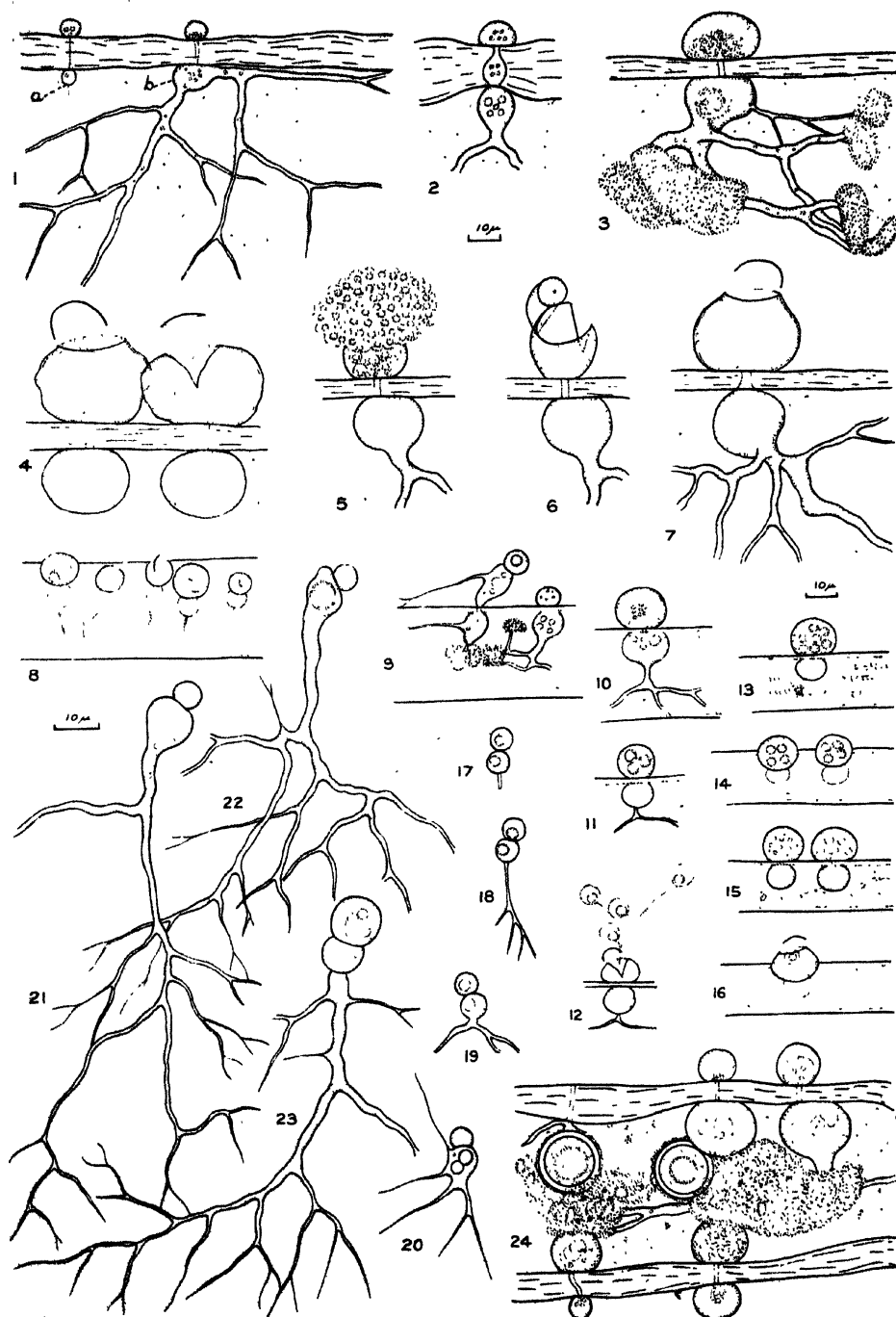
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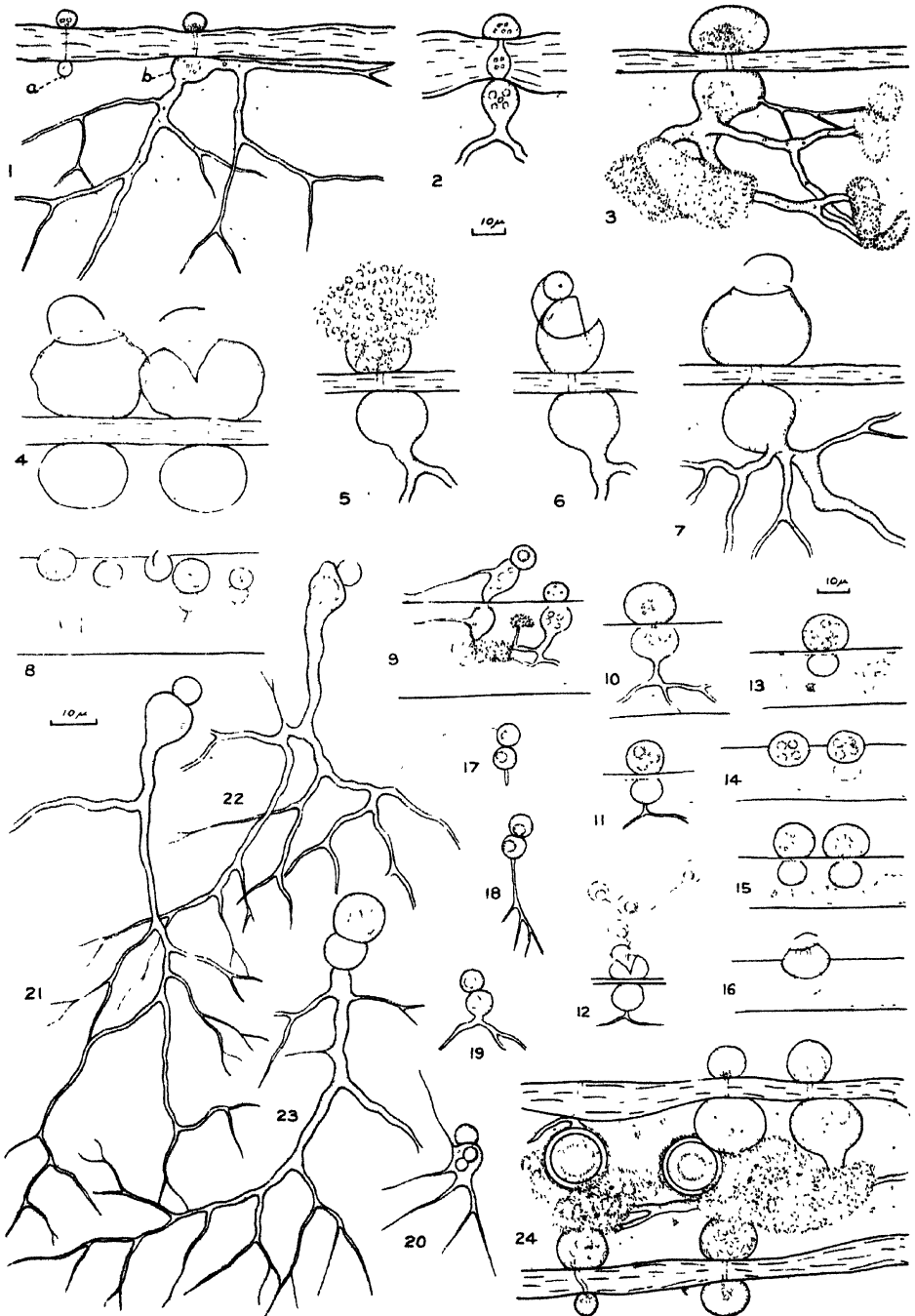
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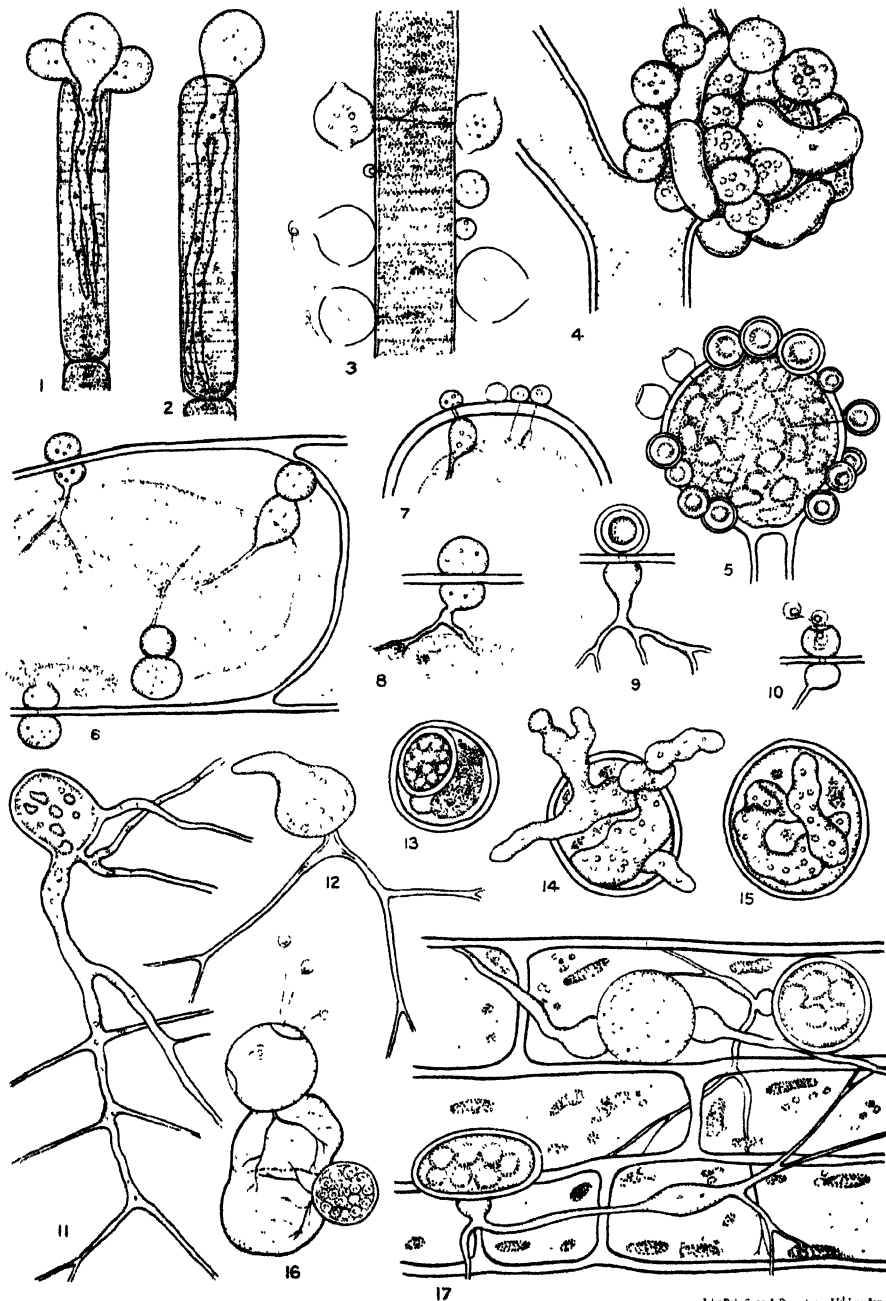


John R. S. &amp; D. J. D. 1944 London





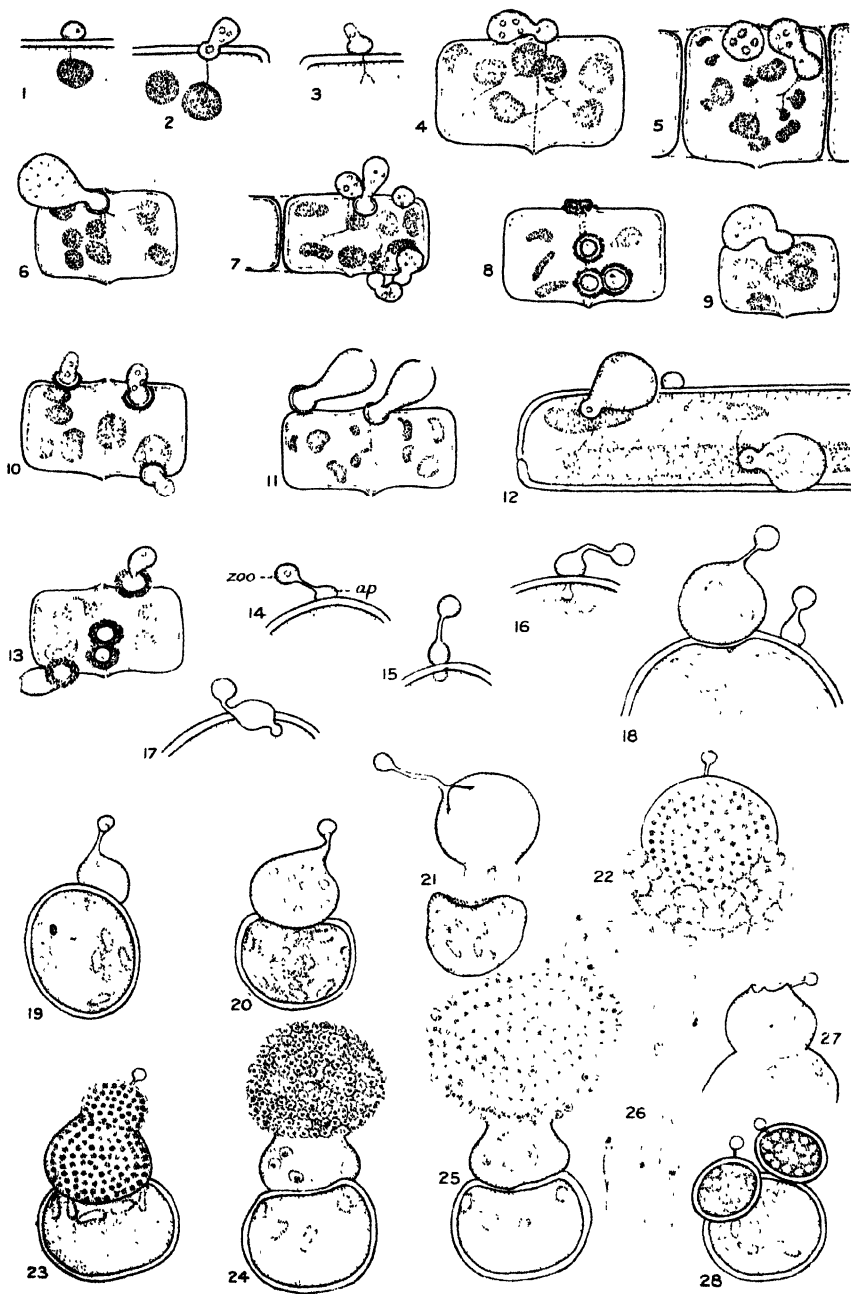




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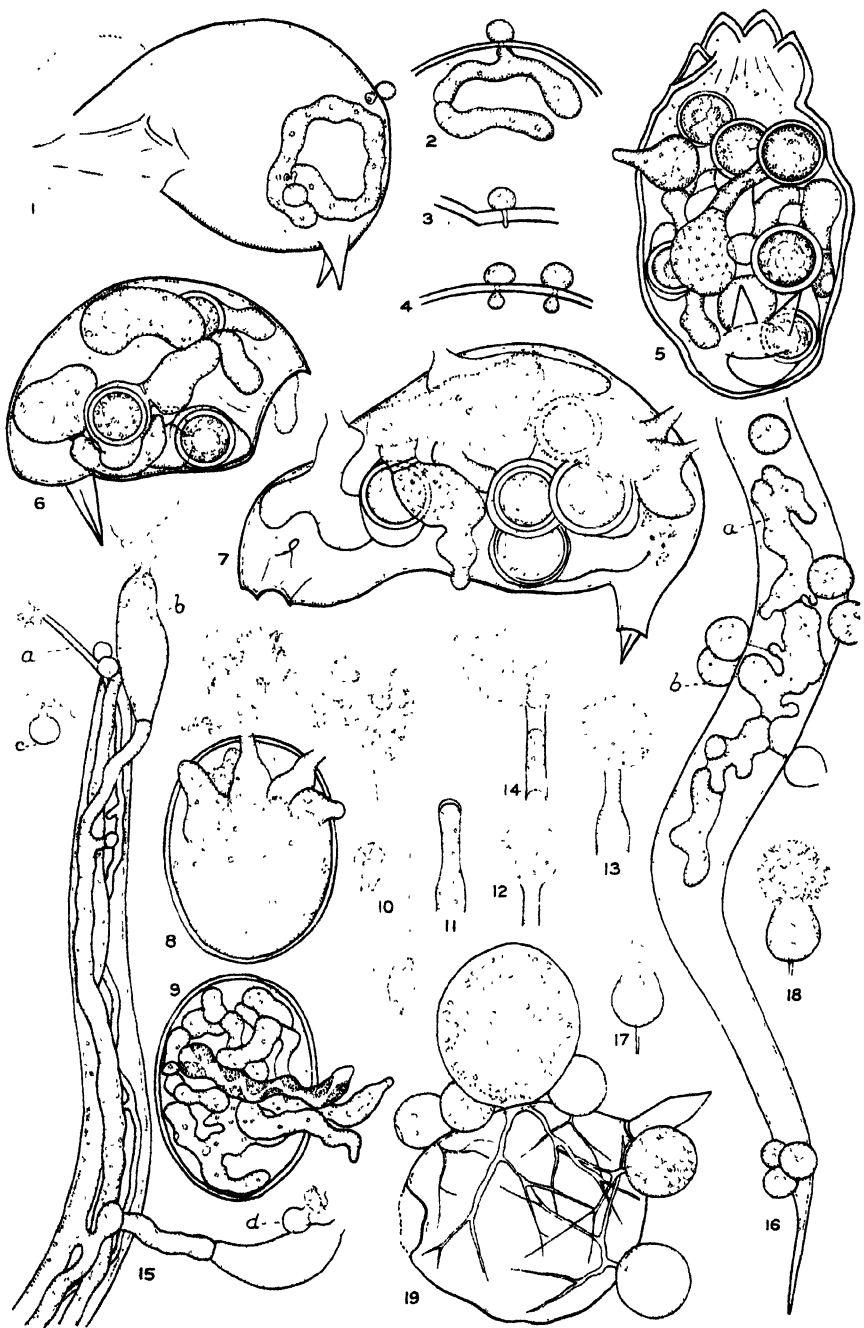






John Sparrow & Davidson, 1912, London





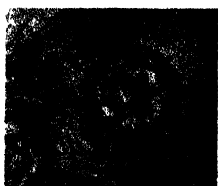
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14

*John R. B. & D. H. B. 1911*



- Figs. 7-9. Sporangia of (?) *Entophlyctis apiculata* in resting cells of *Euglena*. Emergence of zoospores shown in fig. 7.  $\times 866$ .  
 Figs. 10, 11. *Entophlyctis*-like fungus in *Spirogyra*.  $\times 630$ .  
 Fig. 12. Empty sporangium of *Olpidium* sp. in *Spirogyra*.  $\times 530$ .  
 Fig. 13. Discharging sporangia and resting spore of *Entophlyctis Cienkowskians* in *Spirogyra* from Wicken Fen.  $\times 530$ .  
 Figs. 14, 15. Stages in the liberation of the zoospores.  $\times 530$ .  
 Figs. 16, 17. Discharged sporangia and resting spores in *Spirogyra* from Streighton.  $\times 530$ .  
 Fig. 18. Sporangia of *Entophlyctis rhizina* (?) in *Vaucheria* from Streighton.  $\times 630$ .  
 Fig. 19. Prosporangium of *Polyphagus* containing a mature sporangium of *Pleolpidium* (*Rozella*) *Polyphagi*, sp. n.  $\times 630$ .  
 Fig. 20. Discharge of zoospores of same species.  $\times 630$ .  
 Fig. 21. Typical resting spore of *Polyphagus* formed by material from Cambridge.  $\times 530$ .  
 Fig. 22. Resting spore formed by Danish material of same species.  $\times 530$ .

## PLATE 15.

Figs. 1-11.—*Chytridium olla* on oogonia of *Nitella*.

- Fig. 1. Discharged sporangia showing branching of rhizoids within egg.  $\times 530$ .  
 Figs. 2-4. Sporangia with peculiar flame-like outgrowths.  $\times 530$ .  
 Fig. 5. Discharged sporangia showing unbranched nature of rhizoids before entering contents of egg.  $\times 530$ .  
 Figs. 6-8. Stages in the discharge of the zoospores.  $\times 530$ .  
 Fig. 9. Active zoospores, the one on the left exhibiting amoeboid motion.  $\times 530$ .  
 Fig. 10. Large ornamented sporangium.  $\times 530$ .  
 Fig. 11. Intramatrical resting spore with tubular attachment to outer surface of oogonium.  $\times 630$ .  
 Figs. 12, 13. Mature sporangia of *Chytridium appressum* on *Melosira*.  $\times 630$ .  
 Fig. 14. Discharge of zoospores.  $\times 630$ .  
 Fig. 15. Sporangium and resting spore of *Chytridium Schenkii* on *Oedogonium*.  $\times 530$ .  
 Fig. 16. Discharged sporangia.  $\times 530$ .  
 Fig. 17. Sporangium of unusual shape formed by same species.  $\times 630$ .  
 Fig. 18. *Chytridium chaetophilum* (upper) and an immature species of *Entophlyctis* on *Bulbochaete*.  $\times 630$ .  
 Fig. 19. Discharged sporangium of *Chytridium inflatum* on *Oedogonium*.  $\times 630$ .  
 Fig. 20. *Chytridium* (?) sp. on unicellular alga from Site 4.  $\times 630$ .

Figs. 21-26. *Chytridium* (gen. nov. ?) on decaying twigs. All  $\times 530$ .

- Fig. 21. Discharged sporangium containing a few quiescent spores; imbedded in wood.  
 Fig. 22. Empty sporangium showing operculate character.  
 Fig. 23. Mature sporangium with umbonate operculum.  
 Fig. 24. Sporangium wholly imbedded in woody tissue.  
 Fig. 25. Sporangium with a portion of rhizoidal system attached.  
 Fig. 26. Large sporangium partially removed from matrix.

## PLATE 16.

*Chytridium lagenaria*.

- Fig. 1 a. Early stage in development of thallus.  $\times 400$ .  
 Fig. 1 b. Later stage, rhizoidal system well developed, practically no enlargement of sporangial fundament.  $\times 400$ .

- Fig. 2. Unusual case of development of apophysate structure in wall of host as well as in utricle.  $\times 400$ .
- Fig. 3. Nearly mature thallus showing stoutness of intramatrical system.  $\times 400$ .
- Fig. 4. Discharged sporangia showing different types of opercula formed and splitting of wall; the plants apparently devoid of a rhizoidal system.  $\times 400$ .
- Fig. 5. Discharge of zoospores from sporangium.  $\times 400$ .
- Fig. 6. Same sporangium after dispersal of spores, showing fracturing of sporangial wall.  $\times 400$ .
- Fig. 7. Typical discharged sporangium.  $\times 400$ .
- Figs. 8-12. Stages in the life-history of the same fungus growing on *Spirogyra*.  $\times 550$ .  
(Note difference in magnification.)
- Figs. 13-16. Same fungus growing on *Oedogonium*. (Note difference in magnification.)  $\times 400$ .
- Fig. 17. Active zoospore making contact with germinated one.  $\times 550$ .
- Figs. 18, 19. Further stages in the pairing of the spores.  $\times 550$ .
- Fig. 20. Merging of contents of apical spore with that of lower one. The two globules of the spores are clearly visible.  $\times 550$ .
- Figs. 21-23. Types of thalli produced by paired spores after one week in water mounts.  $\times 550$ .
- Fig. 24. Thalli and resting spores in *Rhizoclonium*.  $\times 400$ .

## PLATE 17.

- Figs. 1, 2. Immature sporangia of *Rhizophidium subangulosum* on *Oscillatoria*.  $\times 530$ .
- Fig. 3. Sporangia of *Rhizophidium globosum* on *Oscillatoria*.  $\times 630$ .
- Fig. 4. Sporangia of *Rhizophidium carpophilum* parasitizing oogonium of *Dictyuchus monosporus*.  $\times 630$ .
- Fig. 5. Resting spores and empty sporangia.  $\times 630$ .
- Figs. 6-10.—*Phlyctochytrium laterale*, sp. n. All  $\times 530$ .
- Fig. 6. Immature sporangia of fungus on *Spirogyra*.
- Fig. 7. Early stages in formation of thalli.
- Fig. 8. Mature thallus.
- Fig. 9. Type of resting spore associated with sporangia.
- Fig. 10. Discharge of zoospores.
- Fig. 11. Rhizidiaceous fungus found among vegetable debris.  $\times 630$ .
- Fig. 12. Another undetermined Rhizidiaceous fungus from same material.  $\times 630$ .

Figs. 13-15.—*Lagenidium* (?) sp. in resting cysts of *Euglena*.

- Fig. 13. Resting spore possibly belonging to fungus.  $\times 860$ .
- Figs. 14, 15. Immature thalli.  $\times 860$ .
- Fig. 16. *Rhizophidium globosum* on *Typha* pollen.  $\times 630$ .
- Fig. 17. *Nowakowskiella elegans* in leaf of *Elodea*, showing peculiar thick-walled 'resting' sporangia.  $\times 530$ .

## PLATE 18.

Figs. 1-13.—*Rhizidiopsis emmanuelensis* Sparrow.

All save fig. 12 on *Melosira*. All  $\times 860$ .

- Fig. 1. Encysted zoospore on surface of host cell; delicate penetration tube formed.
- Figs. 2, 3. Beginning of outgrowth which will become main body of sporangium.



- Figs. 4, 5, 9. Nearly mature sporangia.  
 Fig. 6. Large, nearly mature sporangium.  
 Fig. 7. Immature sporangia and germinating resting spore.  
 Fig. 8. Resting spores.  
 Figs. 10, 13. Resting spores germinating.  
 Fig. 11. Empty sporangia formed from germinated resting spores.  
 Fig. 12. Sporangia on *Nitzschia* (?).

Figs. 14–28.—*Scherffeliomyces parasitans*, nom. nov., on *Euglena* cysts.

- Fig. 14. Germinated zoospore (zoo.) on the tip of the germ tube of which a small appressorium has been formed, which is anchored to the outer surface of the host wall.  $\times 1260$ .  
 Figs. 15, 16, 17. Same, showing bulbous intramatrical portion formed by appressorium.  $\times 1260$ .  
 Figs. 18–20. Stages in the transformation of the appressorium into a sporangium. Fig. 18,  $\times 1260$ ; figs. 19, 20,  $\times 860$ .  
 Fig. 21. Nearly mature sporangium with discharge papilla. The plant has been torn from the host cell and reveals the intramatrical digitations.  $\times 860$ .  
 Fig. 22. Mature sporangium.  $\times 860$ .  
 Figs. 23–25. Stages in the discharge of the zoospores.  $\times 860$ .  
 Fig. 26. Forms assumed by zoospore during periods of amoeboid movement.  $\times 860$ .  
 Fig. 27. Empty sporangium.  $\times 860$ .  
 Fig. 28. Resting spores.  $\times 860$ .

#### PLATE 19.

Figs. 1–14.—*Myzocyrtium zoophthorum*, sp. n.

- Fig. 1. Living rotifer infected by fungus. The animal has been injured in mounting.  $\times 530$ .  
 Fig. 2. Thallus established in the body; cystospore adherent to outside of shell.  $\times 530$ .  
 Fig. 3. Early stage in the penetration of the zoospore.  $\times 530$ .  
 Fig. 4. Early stage in establishment of thallus.  $\times 530$ .  
 Figs. 5–7. Heavily infected animals containing both sporangia and resting spores.  $\times 530$ .  
 Fig. 8. Zoospores just liberated from sporangia formed within the egg.  $\times 530$ .  
 Fig. 9. Heavily infected egg showing nature of mycelium and several emerged evacuation tubes of sporangia.  $\times 530$ .  
 Fig. 10. Free swimming zoospores. Free hand.  
 Fig. 11. Modified tip of the sporangium just prior to discharge.  $\times 530$ .  
 Figs. 12, 13. Initiation of spore discharge.  $\times 530$ .  
 Fig. 14. Later stage in spore discharge showing the swarmers escaping as separate bodies.  $\times 530$ .  
 Fig. 15. Portion of a nematode cadaver showing a mixed infection by *Aphanomyces* sp. (a), *Saprolegnia* sp. (b).  $\times 300$ ; emergence of secondary spore of *Aphanomyces* (c), *Saprolegnia* (d),  $\times 530$ .  
 Fig. 16. Another portion of same animal showing *Lagenidium* sp. (a), *Rhizophidium sphaerocarpum* (b). The hyphae of the larger moulds have not been drawn.  $\times 300$ .  
 Figs. 17, 18. Stages in the liberation of the zoospores of *R. sphaerocarpum*; from material on the nematode.  $\times 530$ .  
 Fig. 19. *Rhizophidium globosum* on Rotifer.  $\times 530$ .

## PLATE 20.

All from fixed and killed material mounted in glycerine and stained with eosine.

- Fig. 1. Proliferated sporangia of *Gonapodya prolifera*.  $\times 270$ .  
Fig. 2. Sex organs of *Rhipidium americanum*. Turning the photograph so the left side is lowermost, the androgynous antheridial branch may be seen on the right arching and making contact with the base of the oogonium; within the latter is the rough-walled resting spore.  $\times 330$ .  
Fig. 3. Sporangia of *Blastocladia prolifera*, showing proliferation.  $\times 270$ .  
Fig. 4. *Blastocladia glomerata*, sp. n. Habit of plant.  $\times 55$ .  
Fig. 5. Plants of *Blastocladia Pringsheimii*, showing sporangia, setae, and resting spores.  $\times 55$ .  
Fig. 6. Peltate thallus of *Rhipidium europaeum*.  $\times 80$ .  
Fig. 7. *Blastocladia ramosa*. Habit of plant, showing broadly fusiform sporangia and truncate resting spores.  $\times 110$ .  
Fig. 8. *Gonapodya polymorpha*. Portion of a plant showing proliferated sporangia.  $\times 270$ .  
Fig. 9. Two nearly complete plants of *Blastocladia glomerata*; the hold-fast system has been torn off in mounting.  $\times 55$ .  
Fig. 10. Oospore of *Rhipidium europaeum*; the diclinous antheridium is attached to the lower part of the oogonial wall.  $\times 330$ .  
Fig. 11. Mature oospore of *Sapromyces Reinschii*, showing apically applied, diclinous antheridium.  $\times 330$ .  
Fig. 12. Sporangium of *Pythiogeton* sp. with discharge tube which has pierced the wall of the host (*Achlya* sp.); associated with it are immature resting spores.  $\times 270$ .  
Fig. 13. Habit of plant of *Blastocladia prolifera*.  $\times 110$ .  
Fig. 14. Portion of a plant of *Blastocladia rostrata*. Apiculate and non-apiculate resting spores as well as fusiform sporangia may be seen.  $\times 110$ .

The seasons in a tropical rain-forest (New Hebrides). Part 2. Botany.  
By JOHN R. BAKER, M.A., D.Phil., and INA BAKER. (From the Department of Zoology and Comparative Anatomy, Oxford.) (Communicated by Professor E. S. GOODRICH, F.R.S., F.L.S.)

(PLATE 9)

[Read 7 November 1935]

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Polyploidy in *Tulipa*. By Sir A. DANIEL HALL, K.C.B., F.R.S.; Director, John Innes Horticultural Institution, Merton, London. (Communicated by Professor F. E. WEISS, F.R.S., F.L.S.)

[Received 5 February 1936; read 12 November 1936]

GUIGNARD (1) in 1900 was the first to determine the chromosome complement in *Tulipa*, and found in the three species he examined the haploid number of 12. De Mol (2) in 1925, working with the varieties of the garden tulips, discovered polyploidy in the genus when he found that the variety Pink Beauty was a triploid with 36 chromosomes. In a later paper (3) De Mol stated that after subjecting the bulbs to heat, diploid male gametes could be found: presumably the occasional triploids had arisen through the entry of one of these unreduced cells into the sexual process.

In 1927 W. C. F. Newton (4) published his examination of the species, and in this and a second paper in collaboration with Darlington (5) in 1929 are described triploids, tetraploids, and one pentaploid. His work has since been continued at the John Innes Horticultural Institution, where a collection has been formed embracing such species as are available in commerce together with many others obtained by the assistance of correspondents in their countries of origin. In all cases the counts have been made from root-tip preparations. In *Tulipa* meiosis takes place in the apparently dormant bulb at times varying with the species between September and March; consequently a large number of bulbs of any species has to be destroyed in order to obtain material in the right stage of development. Thus determinations of the haploid number have been made only in a few instances, though Miss M. B. Upcott (6) has devised a technique by which they can be observed in the tube of a germinating pollen grain.

The numbers ascertained for 71 species are set out in the Appendix, and the genus has now been so fully explored as to permit a discussion of the results. Actually over two hundred species find a place in the 'Index Kewensis', but synonyms abound. Many of the species are highly polymorphic, and, since individuals may multiply freely by asexual means, clonal populations have often established themselves as geographical subspecies and have been described as species. As regards taxonomy, the difficulty is increased by the fact that anything beyond the coarsest discriminations are impossible with herbarium material; valid distinctions can be established only by comparison of living specimens. With the exception of a few Central Asiatic species, of which we have not succeeded in obtaining living material, the species here described pretty well cover the genus.

The basic number of chromosomes in *Tulipa* is 12, the only apparent exception being *T. galatica*, in which Newton found 32 as the somatic number. The extra chromosomes have now been found to be supernumerary small chromosomes which do not form part of the regularly inherited complement (Darlington, unpublished), and vary in number in the same plant (Upcott, unpublished). Certain differences in the morphology and size of the chromosomes of different species exist, of taxonomic value.

The genus is divided into two main groups, the Eriostemones and the Leio-stemones. The Eriostemones are distinguished by possessing a little boss clothed with a tuft of hairs at the base of the filaments; the lower part of the three outer tepals is fringed with similar hairs, the leaves are long, narrow, and channelled, all springing from ground-level; in well-grown specimens two or more flowers are carried on separate pedicels, also springing from ground-level. The flowers generally show colour at an early stage, even as the buds emerge from the ground; they are nodding, at least in the bud stage, and show a distinctive urn-shaped profile and usually open widely to a star. Numerous trials have failed to effect any cross between species of the Eriostemones and of the Leio-stemones.

Among the Eriostemones Newton found two tetraploids, *T. silvestris* and *T. Whittallii*. *T. silvestris* is presumably derived from the diploid *T. australis* (syn. *Celsiana*, *fragrans*, &c.) with which it has often been confused in the Floras, though Solms-Laubach (7) pointed out the difference in the distribution of the two species. *T. australis* is truly wild in the Apennines, southern France, Spain, and Portugal, the only tulip indigenous to Western Europe. *T. silvestris* is a denizen along the Mediterranean, often as a weed of the vineyards; as a stray from cultivation it persists in meadows in several English localities. One or two forms can be distinguished on close examination; particularly one from the neighbourhood of Tabriz and N.W. Persia, where it is truly wild. *T. silvestris* shows relatively low fertility, evidence that it is an auto-tetraploid that has arisen by the doubling of a somatic cell and not by hybridization. *T. Whittallii* probably bears the same relation to the very variable Grecian species, *T. Orphanidea*, as *silvestris* bears to *australis*. Two forms, distinct in colouring, are in cultivation. Another presumed association exists between *T. biflora* (diploid) from southern Russia and *T. turkestanica* (tetraploid) from further east. *T. turkestanica* was described by Newton as diploid, an accident due to the fact that the stocks in commerce are mixed and the two species closely resemble one another.

The Eriostemones also include a highly polymorphic species to which many names have been given, as *T. humilis*, *pulchella*, *violacea*, &c. The Cretan tulip, *T. saxatilis*, which has been in cultivation for three centuries and was described by Parkinson, is a triploid belonging to this group. Its diploid analogue is the Mount Ida tulip, *T. cretica*, but a tetraploid form as yet unnamed has recently been found in material collected in Crete by Mr. G. P. Baker.

On general taxonomic grounds certain groups may be distinguished among the

Leiostemones, most of which, however, share the common character of possessing an upright stem, carrying one or more narrow pointed leaves above the two broad basal leaves and an erect flower, which in the bud state is green and only develops colour shortly before it opens.

A very distinct group of narrow-leaved upright tulips may be associated with *T. Clusiana*, and has its habitat in the mountainous country of Iraq, Western Persia, and the Himalayas as far east as Kashmir. This group includes *T. Clusiana* DC. and var. *chitralensis*, *T. stellata* Hook., *T. chrysantha* of gardens (not of Boissier), *T. linifolia* Regel, *T. Batalini* Regel, and *T. montana* Lindley (*T. Wilsoniana* Hoog). Newton determined the pentaploid character of *T. Clusiana*, a species which though of eastern origin has become naturalized along the northern side of the Mediterranean. Before his death he had ascertained that a species from Chitral, introduced under the name of *T. chitralensis* and barely if at all distinguishable from *T. Clusiana*, is tetraploid. The John Innes collection also includes a single bulb, originally given by the late W. R. Dykes, which looks like a dwarf form of *Clusiana* and proves to be diploid. The provenance of this bulb is unknown, beyond an attribution to Tibet; Dykes's sudden death occurred before its importance was known and no record of its source could be traced in his notes. No other specimen of this species has yet been found either in material collected from Upper India or among herbarium specimens. In 1931 the bulb flowered and spontaneously produced a capsule of viable seed, though previous attempts to use it as a parent, either male or female, had failed. The resulting seedlings prove to be triploid, presumably self-fertilization preceded by a failure of reduction on the female side had occurred, since a later successful cross with the tetraploid form has yielded seedlings with varying numbers of chromosomes between diploid and tetraploid (Upcott & La Cour, 1936). The pentaploid *Clusiana*, though grown in quantity for commerce, is generally regarded as sterile, as might be expected from its pentaploid constitution. Reputed seedlings have, however, been received from two trustworthy sources, and on one or two occasions the specimens at Merton set seed spontaneously, though previous attempts to cross them had failed. The reputed seedlings have proved to be pentaploid, but those originating at Merton are aneuploids with 50-52 chromosomes.

*T. stellata* is a hill-species which ranges from Afghanistan to Kashmir, and is associated with a form differing only in possessing a yellow instead of a white basic colour, known in gardens as *T. chrysantha*. This species is tetraploid, and both in external and chromosome morphology it approaches the tetraploid *Clusiana*, from some of the forms of which it is barely to be distinguished. A common origin may be presumed, though among a collection of bulbs recently received from Kashmir has been found a small yellow diploid tulip, as yet unnamed, which may be the origin of the tetraploid *chrysantha* variety. The other species of this group, *T. linifolia* and *T. Batalinii*, and *T. montana*, are diploids. They possess certain distinctive chromosomes which agree with those of the *Clusiana* type.

Next comes a somewhat indefinite group of tulips from Siberia, of which but few are known in cultivation and whose affinities have been but little studied. They are mostly small-flowered tulips, sometimes with more than one flower on separate pedicels, and possess relatively broad leaves. *T. Korolkowi* is a diploid and is associated by name at least with a tetraploid species *T. Korolkowi concolor*, of the provenance of which little is known. The chromosome morphology indicates that the association of these two forms may be correct. *T. Kolpakowskiana* is a widely distributed species, of which a tetraploid form, *T. Kolpakowskiana coccinea*, has recently appeared in commerce from the Soviet agency for the sale of Asiatic bulbs.

Amongst the *Leiostemones* with large flowers and broad leaves one extensive group ranges from Persia to Asia Minor, some members of which have long been naturalized along the northern coast of the Mediterranean. The group is characterized by scarlet or scarlet-crimson flowers possessing an olive or black blotch at the base, often margined with yellow, and more specifically a woolly coating of felted hairs between the tunic and the bulb proper. The taxonomy of these scarlet tulips of the Near East is hopelessly confused; the name most commonly employed, *T. montana* Lindl., was originally attached, as far as can be judged from the evidence available, to a species of another group. Undoubtedly several geographical subspecies can be distinguished which breed approximately true, but the diploid forms merge insensibly into the other forms and no rigid criteria for discrimination can be laid down. Until their distribution can be studied in more detail, together with the local range of variation, it is perhaps best to include them under the earliest name applied, i.e. *T. oculus-solis* St. Amans. Two species have long been naturalized in Italy and on the Riviera, the typical *T. oculus-solis* and *T. praecox* Tenore. They have been much confused in the Floras, though Tenore's diagnosis affords an accurate means of discrimination, and *T. praecox* proves to be a triploid. Other triploids also occur, e.g. from Syria a handsome form easily distinguishable from *praecox*, which is possibly the species found in herbaria under the name *T. alypiensis*. In the John Innes collection are at least two other triploids belonging to this group, from Asia Minor and Palestine respectively, which can only speculatively be assigned to described species. Probably other triploids belonging to this group will be discovered with a limited local distribution, clones with little or no power of sexual reproduction. Finally, at the extremity of the range of the group, in Persia and Turkestan, is found the triploid *T. lamata*, one of the largest and most handsome of all tulips, which reached this country in the first instance from Kashmir, where it is an introduction grown on the roofs of temples.

The hypothetical *T. Gesneriana* Linn., the name assigned to the garden tulip complex, has yielded no polyploids among the wild and semi-wild forms, though among the cultivated varieties five more triploids have been added to the three identified by de Mol. Of about fifty varieties examined eight are triploid, the rest diploid. A certain number of seedlings with the triploid as one parent



have been obtained at Merton, and some of these have been found to be aneuploid, e.g. with from 24 to 34 chromosomes, though no aneuploids have before been observed either in species or garden varieties. These aneuploids will be dealt with elsewhere.

Among the large-flowered species from Central Asia, *T. Fosteriana*, *Griegii*, *Kaufmanniana*, &c., only diploids have been observed.

Finally, at the extremity of the range of the genus one species, *T. edulis*, with a variety distinguished as *T. latifolia*, is found in Japan and appears to be identical with a species from the Chinese mainland described by Baker as *T. erythronoides*. This minute tulip, the smallest of the genus, possesses 48 chromosomes, and on account of certain morphological peculiarities, notably two linear bracts a little below the flower, should probably be assigned to a special genus.

*T. galatica* has already been mentioned as being exceptional in possessing eight fragments in addition to its 24 chromosomes, though more extended observation shows that the number is variable (4-11). It is a pale yellow tulip which Newton associated with a scarlet tulip, *T. armena*, from the same region of Asia Minor. Three large families were raised by crossing these two forms, and out of 490 seedlings counted four only were scarlet like *armena*, the rest appeared identical with *galatica*. But the number of fragments varied from 0 to 19, and though the *galatica* type must be associated with fragmentation, even the few seedlings showing the *armena* coloration still possessed fragments. Fragmentation has again been observed in an *oculus-solis* form in commerce as *T. Borszczowii*.

All the polyploids in *Tulipa* are definitely larger in all their parts than the corresponding diploids, though, of course, we have no experimental knowledge that the one has given rise to the other. Further evidence of increased vigour in the polyploids is supplied by their marked habit of emitting stolons, at the end of which a bulb is formed. All tulips possess this habit in some measure; in their early history as seedlings the bulbs invariably form 'droppers' descending in the soil, but it is rare to observe horizontal stolons. The triploid *T. saxatilis* will, however, give rise to an offset bulb 2 feet away from the parent bulb, and most of the other polyploids have the same wandering habit. Without doubt, this habit has helped to secure the wide distribution of some polyploids, as, for example, *T. Clusiana* and *T. praecox*. Both must be essentially clonal populations, for, though *T. Clusiana* has been observed to form seed, there are no reports of seed-formation occurring in nature with either species. The stoloniferous habit might be regarded as a compensating device to make up for sexual sterility. To some extent it may be an expression of polyploid vigour which cannot find its outlet in seed-formation, but the simpler hypothesis is that such triploids as will continue to arise from time to time through accidents in meiosis will possess a small survival value unless at the same time they happen to be also endowed with a marked stoloniferous habit which enables them to extend their range.

The study of the chromosomes of *Tulipa* has proved helpful in the consideration of the taxonomy of the genus. The chromosome morphology does confirm a grouping within the genus based on general morphological grounds, and is critical of some of the classifications that have been proposed. Again, the recognition of polyploidy has cleared up the long-standing confusion between species like *T. australis* and *silvestris*, or *T. oculus-solis* and *T. praecox*.

It still remains a matter of dispute whether the polyploids should be assigned specific names of their own. For example, *T. Clusiana* is pentaploid, the corresponding tetraploid from the N.W. Frontier of India, though it has been named *T. chitralensis*, cannot be distinguished macroscopically from the pentaploid: are the diploid and triploid forms to have specific names? The distinction between diploid and triploid is absolute, something different in kind from that between two closely related species both diploid.

Dr. C. D. Darlington took over the cytological study of the genus after Mr. Newton's death, and with him Miss M. B. Upcott has lately collaborated. Dr. J. Philp was responsible for the hybridizations recorded. Most of the chromosome counts were made by Mr. L. La Cour.

#### SUMMARY.

(1) The chromosomes of 72 species of *Tulipa* have been counted. The majority are diploids ( $n=12$ ), but one pentaploid, ten tetraploids, and six triploids have been discovered.

(2) In one instance the same species has been found to exist in pentaploid, tetraploid, triploid, and diploid forms, the triploid having been produced experimentally by hybridization between tetraploid and diploid.

(3) Aneuploids have been produced experimentally, but are not known among the species or garden varieties. In two species fragmentation has been observed.

(4) The morphology of the chromosomes is of service in determining the taxonomic groups within the genus.

#### APPENDIX.

Number of chromosomes (somatic counts) determined by W. F. C. Newton (N), C. D. Darlington (D), L. La Cour (L), M. B. Upcott (U).

ERICOSTEMONES.	Determined by :	
<i>Tulipa australis</i> Link. ....	2n=24	N
— <i>Griesbachii</i> Borbás .....	24	L
— <i>per-sica</i> hort. ....	24	N
— <i>primulina</i> Baker .....	24	N
— <i>urumien-sis</i> Stapf .....	24	L
— <i>silvestris</i> L. ....	{	48 N
— <i>Orphanidea</i> Boiss. ....		24 N
— <i>Hageri</i> Held. ....		24 N
— <i>Whittallii</i> . Two varieties .....		48 N

## ERIOSTEMONES.

		Determined by :	
<i>Tulipa humilis</i> Herb.	} Numerous varieties .....	24	N
— <i>pulchella</i> Fenzl.			
— <i>violacea</i> Boiss.			
— <i>Aucheriana</i> Baker .....		24	L
— <i>cretica</i> Boiss. ex Held. ....		24	L
— <i>saxatilis</i> Sieber .....		36	D
— unnamed species from Crete .....		48	L
— <i>biflora</i> Pall. Two varieties .....		24	N
— <i>turkestanica</i> Regel .....		48	L
— <i>polychroma</i> Stapf. ....		24	L
— <i>tarda</i> Stapf ( <i>dasytemon</i> ) .....		24	N

## LEIOSTEMONES.

*Clusiana* group.

<i>Tulipa Clusiana</i> DC. Several sources .....	2n=60	N
— — var. <i>chitralensis</i> . Two sources .....	48	D
— — var. of unknown provenance .....	24	D
— — var. produced at Merton .....	36	U
— <i>stellata</i> Hooker. Several sources .....	48	N
— — var. <i>chrysantha</i> . Several sources .....	48	N
— — unnamed species from Kashmir .....	24	L
— <i>montana</i> Lindley ( <i>T. Wilsoniana</i> Hoog) .....	24	L
— <i>linifolia</i> Regel .....	24	N
— — var. <i>Batalinii</i> Regel .....	24	N
— — var. <i>Maximowiczii</i> Regel .....	24	N

*Oculus-solis* group :

<i>Tulipa oculus-solis</i> St. Amans .....	2n=24	L
— — var. <i>montana</i> ( <i>T. montana</i> of the Floras).		
Many sources .....	24	L
— <i>Stapfii</i> Turrill. Two sources .....	24	L
— <i>cypria</i> Stapf. ....	24	L
— <i>undulatifolia</i> Boiss. ....	24	L
— <i>cuspidata</i> of Stapf (?). Received as <i>cuspidata</i> from van Tubergen) .....		
— <i>kuschkensis</i> Fedtsch. ....		
— <i>Schmidtii</i> Fomin .....		
— unnamed species, S. H. ....		
— <i>praecox</i> Tenore .....		
— <i>aleppensis</i> Boiss. ex Regel (?), from Syria,		
— unnamed Palestine species, D. 50 .....		
— <i>lanata</i> Regel. Several sources .....		
— <i>Borszczowii</i> Regel (?). Received as <i>Bor</i> van Tubergen.		

ofessor J. M. Beal.

## LEIOSTEMONES.

*Gesneriana* group :

		Determined by :
<i>Tulipa suaveolens</i> Roth .....	2n=24	L
— <i>armena</i> Boiss. ....	24	N
— <i>galatica</i> Freyn .....	{ 24+4-11 fragments. N, D, U.	
— <i>planifolia</i> Jordan ... ..	24	L
— <i>boeotica</i> Boiss. et Held. ....	24	L
— <i>Gesneriana</i> . Garden varieties—normal number ..	24	L

*Eichleri* group :

<i>Tulipa Eichleri</i> Regel .....	2n=24	N
— <i>Fosteriana</i> Hoog .....	24	L
— <i>Micheliana</i> Hoog .....	24	L
— <i>amabilis</i> Fedtsch. ....	24	L
— <i>Greigii</i> Regel .....	24	N
— <i>Kaufmanniana</i> Regel. Several varieties .....	24	N
— <i>ingens</i> Hoog .....	24	N
— <i>Tubergeniana</i> Hoog .....	24	L
— <i>Hoogiana</i> Fedtsch. ....	24	L
— <i>praestans</i> Hort. Several varieties .....	24	N

*Kolpakowskiana* group :

<i>Tulipa Kolpakowskiana</i> Regel .....	2n=24	N
— — var. <i>Holzeri</i> .....	24	L
— — var. <i>coccinea</i> .....	48	L
— <i>Sprengeri</i> Baker .....	24	N
— <i>Korolkowi</i> Regel .....	24	L
— — var. <i>concolor</i> .....	48	L
— <i>altaica</i> Pall. ....	24	L
— <i>Ostrowskiana</i> Regel .....	24	L
— <i>Kesselringii</i> Regel .....	24	L

*Edulis* group :

<i>Tulipa edulis</i> Baker .....	2n=48	L
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## ERICOSTEMON. Garden Tulips, chromosome numbers determined by L. La Cour.

<i>Tulipa austriaca</i> .....	Amiral de Constantinople .....	Parrot.
— <i>Griesbachii</i> .....	Advance .....	Hybrid.
— <i>persica</i> hort. .....	Alexandra .....	Dutch.
— <i>primulina</i> Baker .....	rethusa .....	Garden.
— <i>urumiensis</i> Stapf .....	echus .....	Dutch.
— <i>silvestris</i> L. .....	tigon .....	Darwin.
— <i>Orphanidea</i> Boiss. .....	Aimable .....	Darwin.
— <i>Hageri</i> Heldr. .....		
— <i>Whittallii</i> .....	two var.	

DIPLOIDS	....	Coffee Colour .....	Parrot.
		Crimson Beauty .....	Early.
		Fantasy .....	Parrot.
		Fire King .....	Darwin.
		Gemma .....	Parrot.
		Inglescombe Scarlet .....	Cottage.
		Isolda .....	Cottage.
		John Ruskin .....	Cottage*.
		La Merveille .....	Cottage.
		La Tristesse .....	Darwin.
		Le Rêve .....	Early*.
		Louis XIV .....	Dutch.
		<i>Lutea major</i> .....	Parrot.
		Mayflower .....	Hybrid.
		Millet .....	Darwin.
		Maarkgraaf van Baden .....	Parrot.
		Mrs. Hoog .....	Cottage.
		Mrs. Moon .....	Cottage.
		Perfecta .....	Parrot.
		Pride of Haarlem .....	Darwin.
		Suzon .....	Darwin.
		White Swan .....	Early.
		Zulu .....	Darwin.
TRIPLOIDS	...	<i>Gesneriana spathulata major</i> .....	Cottage.
		Inglescombe Yellow .....	Cottage*.
		Zomerschoon .....	Cottage.

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\* Haploid number also determined by Professor J. M. Beal.



Observations on the root anatomy of the genus *Aletris*. By H. S. HOLDEN,  
D.Sc., F.L.S., and L. KRAUSE, B.Sc., University College, Nottingham.

(With 27 Text-figures)

[Read 12 November 1936]

THE genus *Aletris*, placed by Bentham and Hooker (3) in the Haemodoraceae, has been constituted the type of the monogeneric subfamily Aletroideae (Liliaceae) in the new edition of Engler-Prantl's 'Natürliche Pflanzenfamilien' (10). The genus appears to be a very natural one with rather a remarkable discontinuous distribution, the majority of the species occurring in Eastern Asia, and ranging from the Himalayas (e.g. *A. nepalensis* Hook. fil. and *A. sikkimensis* Hook. fil.) through China (e.g. *A. foliosa* Max. and *A. japonica* Franch.) to Japan, the Philippines, Java, and Borneo. The two remaining species (*A. farinosa* L. and *A. aurea* Wall.) occur in Eastern North America, the former being more northerly in its distribution than the latter.

All the species have a tough rhizome showing sympodial growth and bearing numerous fine roots. The oldest roots are brown and wiry, and in these the tissues external to the endodermis have often been exfoliated, though they may persist as a loose membranous covering. These roots appear to be survivors from the previous season's growth. The rhizome bears in addition both short relatively stout branch-roots and somewhat more slender ones with numerous branches.

As a preliminary examination (8) of a small supply of material of *A. farinosa* revealed a number of interesting features, it was decided to make a more detailed study of this and other available species. An ample supply of *A. farinosa* was obtained through the kindly offices of Prof. M. Chrysler of Rutgers University, New Jersey. Material of the other North American species, *A. aurea*, was collected by the Charleston Museum. The authors are greatly indebted both to Professor Chrysler and to the staff at Charleston for the readiness with which they responded to requests for material. No adequately preserved material of the various Asiatic species was available, but small portions of herbarium specimens generously presented by Mr. Ramsbottom, Keeper of the Department of Botany of the British Museum, have enabled us to obtain a number of useful data for comparative purposes. The herbarium material examined included roots of the following species :—*A. foliosa*, *A. glabra*, *A. khasiana*, *A. lanuginosa*, *A. nepalensis*, and *A. sikkimensis*. In view of the fact that some uncertainty prevails with regard to the precise specific determination of these Asiatic plants, they will be referred to under the names

given on the herbarium sheets of the British Museum together with any available details of collector and source.

The herbarium specimens offered considerable technical difficulty in manipulation, but were prepared for microscopic examination by a modification of the method recommended by McLean (13). These difficulties recurred to some extent in dealing with the older roots of the American species owing to the extremely tough nature of the endodermis. This was so refractory that ordinary embedding methods were unsuccessful, and we are indebted to Prof. J. M. Thompson and Mr. W. Horton of the Department of Botany of Liverpool University, for several slides prepared by their special technique, and for suggestions which enabled us to evolve a suitable method for our material. The treatment consists in essentials of infiltration with a mixture of paraffin wax and rubber after taking through preliminary grades of n-butyl alcohol into chloroform, the wax containing about 0.5 per cent. of rubber. The rubber solution supplied in collapsible tubes for puncture repairs proved satisfactory. It was added in appropriate quantity to small shavings of wax in a porcelain dish in the embedding oven at 55° C. and heated at that temperature until all the rubber solvent was driven off. The mixture produced was used for infiltration and embedding in the usual way, although a good deal of experimenting was necessary with individual roots to get a mixture which would ribbon satisfactorily. Extremely old roots required preliminary treatment prior to embedding, this consisting of gentle maceration in a mixture of potassium chlorate and strong nitric acid.

In addition to sections, maceration methods were also employed for studying isolated elements. The method suggested by Priestley (15) proved most satisfactory. This consists of two to four hours' maceration in 5 per cent. chromic acid at 55° C., followed by thorough washing until all the yellow colour is discharged. The washed roots are placed in 1 per cent. Gentian Violet solution and washed in 50 per cent. glycerine. Gentle teasing in glycerine enables single elements to be picked out and mounted in glycerine jelly for examination.

#### ALETRIS FARINOSA and A. AUREA.

It has been found impossible from an examination of the material in our possession to differentiate between the two North American species, *A. farinosa* and *A. aurea*, on data derived from the root anatomy. In both species the larger unbranched adventitious roots were studied first.

*The surface layer.*—The surface layer of the root is remarkable in that it does not develop root-hairs. Instead of these the whole of the constituent cells become papilliform and elongated in a plane at right angles to the axis of the root, forming a closely-set series. The free surface of each cell is rounded, and appears to be modified in that in stained preparations this part of the wall stands out very prominently owing to the readiness with which it absorbs dyes. The papilliform character of these cells is obvious at a very early stage, and is clearly seen in sections cut at the level of the base of the root-cap (fig. 1).



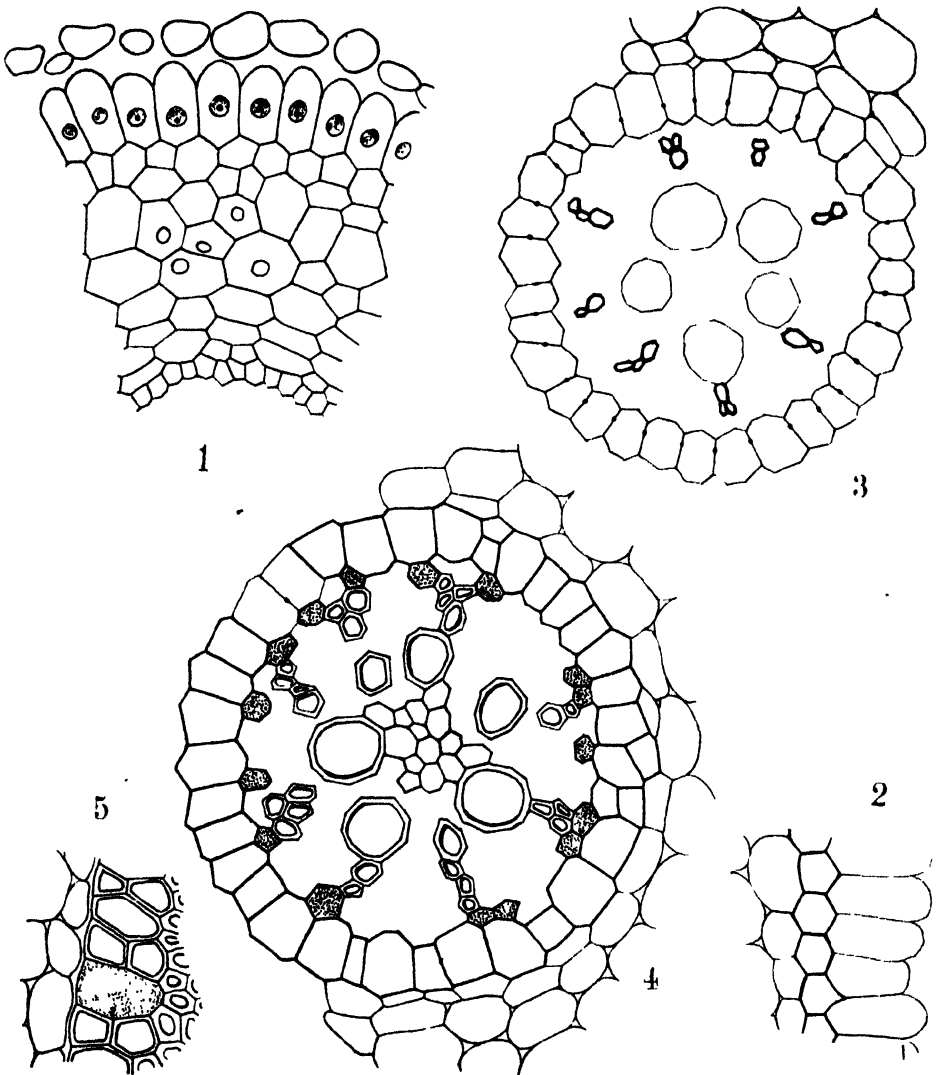


FIG. 1.—Transverse section showing the development of the papilliform surface-cells at the level of the base of the root-cap.

FIG. 2.—Transverse section showing papilliform cells and exodermis.

FIG. 3.—Transverse section, stele just above the base of the root-cap; the endodermis is in the primary condition and the protoxylem is differentiated, though the metaxylem vessels are still thin-walled.

FIG. 4.—Transverse section, stele at a slightly higher level; the xylem elements are all thick-walled and the cells of the pericycle are beginning to thicken; the endodermis, with the exception of two cells, is in the secondary condition.

FIG. 5.—A small portion of the endodermis in the early tertiary stage, showing an isolated passage-cell.

All figures of *A. farinosa*,  $\times 350$ .

In a few examples the cells contained fungal hyphae, but the fact that they are sporadic in appearance and local in distribution suggests that they are not constituents of a mycorrhizal symbiont (fig. 6 *a*).

The layer of cells immediately internal to the surface-layer becomes modified to form a typical exodermis (fig. 2). The remainder of the cortical tissues consists of rounded parenchymatous cells and, apart from the layer of cells immediately external to the endodermis, calls for no special comment. The layer to which reference has just been made is composed of cells characterized

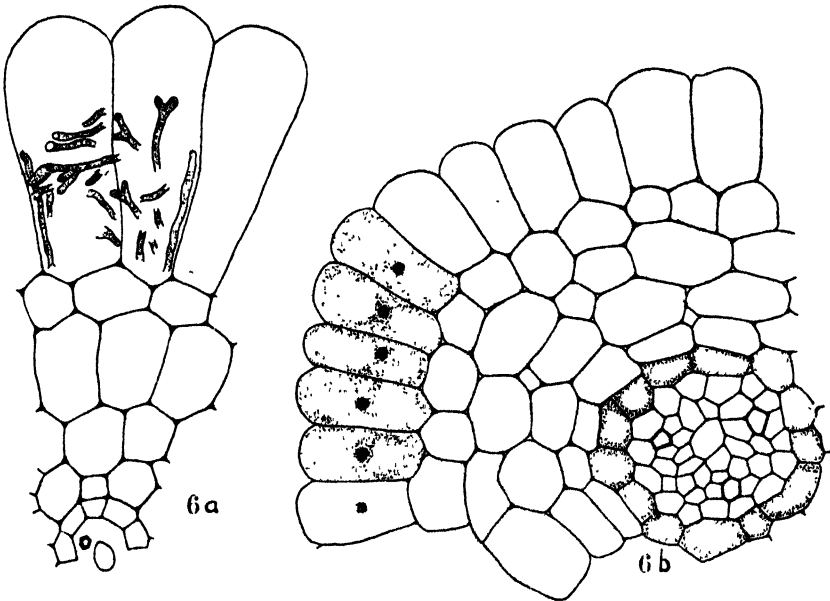


FIG. 6 *a*.—Portion of a transverse section of a small branch-root of *A. aurea*, showing the relatively large size of the papilliform cells and also the presence of fungal hyphae in these cells. ( $\times 300$ .)

FIG. 6 *b*.—Portion of a transverse section of a young branch-root of *A. aurea* cut just above the root-cap; the lignification of the protoxylem has commenced and the single cell in the centre of the root destined to become the metaxylem vessel can be distinguished. ( $\times 300$ .)

by the considerable thickening of the inner wall. The initiation of this thickening is obvious at a very early stage, preceding the deposition of differentially stainable material in either the endodermis or protoxylem.

*The endodermis.*—The cylindrical stele, when mature, is surrounded by a continuous endodermis, the cells of which are so heavily lignified that the lumen is represented only by a small pore. The lamellae constituting the tertiary thickening are clearly defined and show up without any special treatment (figs. 7, 8). The tertiary layers are traversed by numerous pits which show

most clearly in longitudinal section (fig. 8). They are branched, and appear to communicate with pits in neighbouring endodermal cells, with the adjacent cells of the pericycle, and with those of the cortex. They are most abundant on the inner tangential walls, i.e. those in contact with the pericycle. In the mature roots no passage-cells have been seen in the endodermis. Contrary to the usual condition characterizing endodermal cells, those of the root in

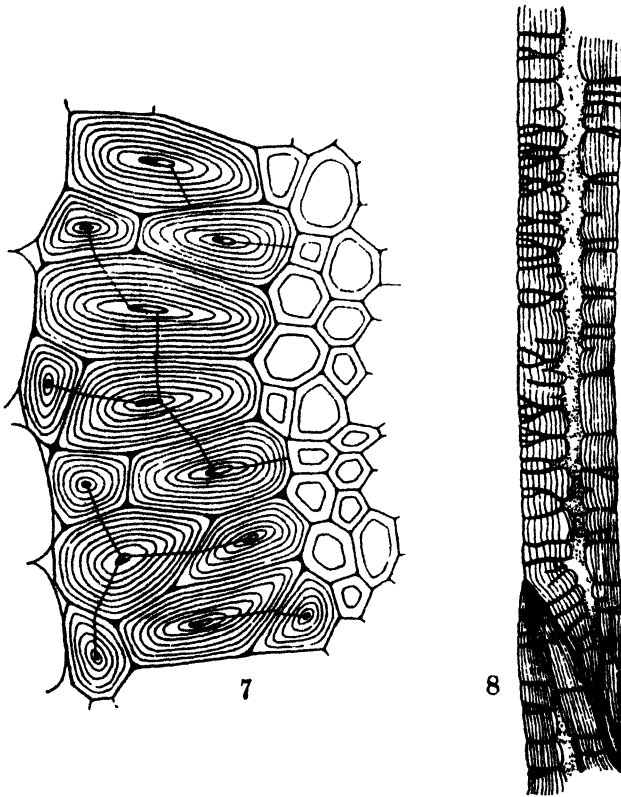


FIG. 7.—Portion of mature endodermis of *A. aurea* in transverse section showing mature tertiary condition. ( $\times 350$ .)

FIG. 8.—Adjacent portions of two mature endodermal cells of *A. farinosa* in longitudinal section. ( $\times 350$ .)

*Aletris* are pointed at the ends resembling prosenchymatous fibres (fig. 8). The ends of the cells overlap considerably, so that the endodermis frequently appears to consist locally of two or three layers of cells (fig. 7). In old decorticated roots the endodermis walls vary in colour from deep brown to golden yellow. The endodermis can be distinguished as a complete ring of small cells at the level of the base of the root-cap. Above the level of the base of

the root-cap is a zone of elongation where the endodermal cells increase considerably in length and slightly in radial width; at this stage the walls are very thin and delicate and preparations collapse very easily.

As thickening begins in the protoxylem the endodermal cells become firmer without any apparent increase in the thickness of the wall. The first sign of endodermal differentiation takes the form of a relatively wide strip on the radial walls, with special staining properties, but without any apparent local increase in thickness of the cell-wall. At a slightly later stage well-defined Casparian strips are visible (fig. 3): these appear to be shorter in radial extent than the unthickened strips which preceded them. This stage is rapidly followed by the development of a suberin lamella in most of the cells (fig. 4). The suberin is deposited first in the cells opposite the phloem groups and spreads a little later to the cells on either side. Passage-cells, in which the primary stage persists, occur outside the protoxylem; these passage-cells are small isolated single or paired cells (figs. 4, 5). Tertiary thickening of the endodermis follows rapidly on the secondary stage and is well marked within 8–10 mm. of the root-tip. The first cells to be lignified in the tertiary stage lie opposite the phloem groups. During the maturation of the endodermal cells the passage-cells begin to undergo a similar type of thickening, and ultimately are indistinguishable in unstained preparations from the rest of the endodermis, so that in the mature root the tertiary endodermis forms a continuous cylinder. The tertiary thickening of the passage-cells begins when the walls of the majority of the endodermal cells have reached about half the thickness they will attain when mature. If sections of the mature root are treated with iodine solution followed by strong sulphuric acid the last few layers deposited in the endodermis are seen to have a higher lignin content than those laid down at the initiation of the tertiary phase, whilst the material laid down on the walls of the passage-cells is all of this more strongly lignified type.

*The pericycle.*—The cells of the pericycle are long, narrow, and square-ended; they retain their contents and are provided with simple pits. In common with other initially parenchymatous intrastelar tissue, the pericycle becomes lignified and thick-walled. The thickening begins after the first lignification of the metaxylem when the endodermis is becoming tertiary, and appears first of all in the cells adjacent to the protoxylem (fig. 4).

*The xylem.*—Although it has been stated (9) that, in Monocotyledons, 'the internal elements of a tracheary nature are completed before those lying further out in the region of the protoxylem', this does not accord with our observations on the roots of *Aletris farinosa* and *A. aurea*. In our material the cells destined to form the large metaxylem vessels are enlarged and stand out clearly from the other stelar tissue at the level of the base of the root-cap. The protoxylem elements become lignified a little way above this level, the lignification of the other tracheary elements following in centripetal order. The lignification of the largest metaxylem elements is completed last of all (fig. 3). The large metaxylem vessels surround a central pith, the cells of which are strongly

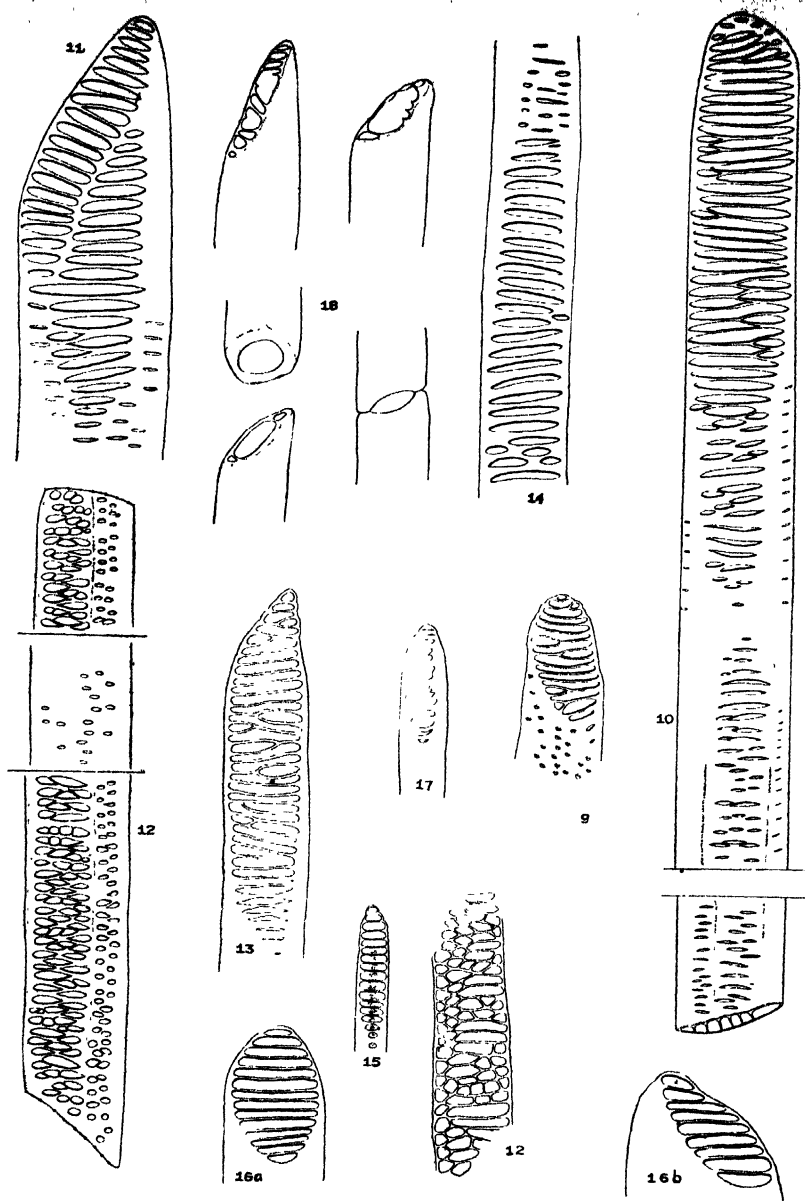


FIG. 9.—Typical end-wall of vessel-segment in *A. farinosa*.

FIGS. 10–14.—Examples of range of variation in method of vessel perforation in *A. farinosa* (see text).

FIG. 15.—End-wall of very young vessel-segment of *A. farinosa* from near the root-tip.

FIG. 16 *a, b*.—End-walls of vessel-segments of *A. glabra* with scalariform perforations.

FIG. 17.—End-wall of vessel-segment of *A. khasiana*, showing degraded scalariform perforation.

FIG. 18.—End-walls of five vessel-segments of *A. nepalensis*, showing different types of perforation.

(All  $\times 400$ .)

thickened in the mature root ; they are separated from each other by narrow strips of thickened ground-tissue. They exhibit a number of features of considerable interest, the most important of which is the nature of the end-wall of the vessel segments. The end-walls vary enormously in length and show a type of perforation ranging from scalariform to scalariform-reticulate (figs. 9–14). This appears to be the first record of the existence of such end-walls in the metaxylem vessel segments of Monocotyledons. According to Jeffrey (9) the Monocotyledons appear to be characterized by porose perforations between the vessel segments. In *Aletris farinosa* and *A. aurea* the commonest type of end-wall is a short and well-defined wall with scalariform perforations (fig. 9) ; the transverse bars are wider at the base than in the middle. A number of variants of the more generally occurring type call for special comment. The simplest of these is one in which the end-wall is transverse or nearly so ; here the perforation is also of the simple scalariform type (fig. 10). In a second type the end-wall appears to develop a double scalariform perforation ; each of the scalariform systems appears to run independently apart from one or very few common perforations, and it is suggested that this condition may be due to vessels of unequal diameter coming into contact with the segment in question (fig. 11).

What appears to be a much more remarkable type of perforation, also scalariform in type, is occasionally met with. This extends from end to end of an individual segment, being confined to one of the plane walls of the vessel. Portions of an example of this kind are illustrated in fig. 12, which also shows the normal type of pitting found on the other walls of the vessel. Occasionally the end-wall of a vessel is inclined so steeply that it is difficult to define its limits as the slit-like perforations are continued with relatively insignificant gaps along the face of the vessel (figs. 10, 14). Xylem elements of a similar appearance are figured by Brush (5) in *Platanus Wrightii*. In other vessels, too, the slit-like perforations show a gradation to the normal type of pitting on the side-walls of the vessel (fig. 14).

Macerations of the stele near the root-tip show that the scalariform perforations on the end-walls of the vessel segments of the metaxylem are present, whilst these are still thin-walled and contain abundant cytoplasm. At this stage the scalariform perforations differ strikingly from those in the mature vessels. The transverse bars are very thin and the pores are relatively wide with rounded ends (fig. 15). The most remarkable difference is at the margins of the perforations—these, in the young root, being rounded, whilst they are definitely slit-like in the mature metaxylem elements.

*The phloem.*—The structure of the phloem calls for no special comment, Typically there is one sieve-tube in each group surrounded by companion cells which abut directly on the pericycle.

*The branching roots.*—In addition to the stout roots, the anatomy of which has been described above, the rhizome bears numerous roots which branch freely. These vary considerably in size, the largest ones approximating in

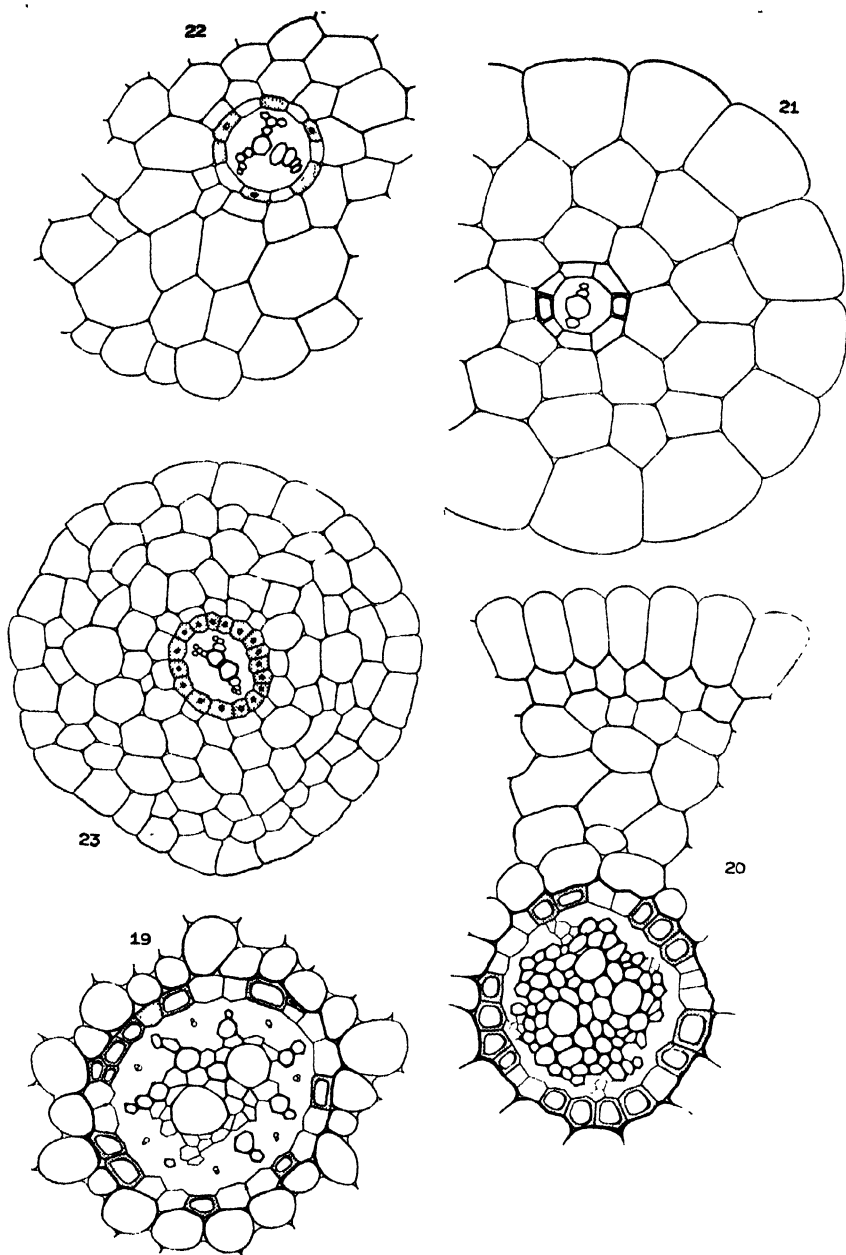


FIG. 19.—Transverse section, stele of branch-root of *A. farinosa* just above base of root-cap. Note the two large centrally placed metaxylem vessels and the various stages of development shown by the endodermis.

FIG. 20.—Transverse section, part of mature branch-root of *A. nepalensis*. The ground-tissue is lignified and the endodermis is partly secondary and partly tertiary.

FIGS. 21, 22, 23.—Small branch-roots of *A. farinosa*, *A. lanuginosa*, and *A. khasiana*, showing endermal characters and solid diarch and triarch xylem groups.

(Figs. 19 & 20,  $\times 250$  ; figs. 20-23,  $\times 300$ .)

diameter to the unbranched roots, whilst the smaller ones are half this diameter or less. In their general anatomical characters they are essentially the same as the roots already described.

The most obvious variation lies in the distribution of the large metaxylem vessels, and this seems to be correlated in a measure with the size of the root concerned. In smaller roots the number of the metaxylem vessels is reduced to two or three, and these are located in the centre of the root with the consequent elimination of the pith. Only one example has been found of a large metaxylem vessel in the medulla of a stout unbranched root.

*The lateral roots.*—These differ from the parent roots in a number of particulars. In the first place, the relative size of stelar to extra-stelar tissue is much less, the papilliform cells being equal in size to those of the main roots (figs. 6, 21–23). The cortical cells are also large and the endodermis shows a characteristic lag in the rate of development of the tertiary condition. The primary endodermis may persist for a length of 2 cm. from the root-tip, although it is common to find isolated endodermal cells opposite the phloem groups in the tertiary condition. Further development of the secondary and tertiary condition is very leisurely, although the endodermis is completely tertiary in roots which we judge from their appearance to be of the previous year's growth (fig. 23). The pericycle remains parenchymatous for a considerable time, but is thickened in the fully mature root. The stele is normally triarch, though occasionally tetrarch, with, typically, a large metaxylem vessel in the centre of the stele; in some of the larger roots there may be two or three vessels (fig. 19).

*Notes on the anatomy of certain Asiatic species.*

Owing to the fact that these observations are made on small supplies of softened herbarium material, they do not constitute as complete a record as those yielded by the American material, although they show a number of interesting points of difference from these species. As far as our observations go, the roots of all species possess a superficial layer of papilliform cells replacing the piliferous zone, and also the typical tertiary endodermis composed of cells with pointed ends.

*ALETRIS FOLIOSA* Bur. et Franch. (J. Bisset 4081 and 2749).

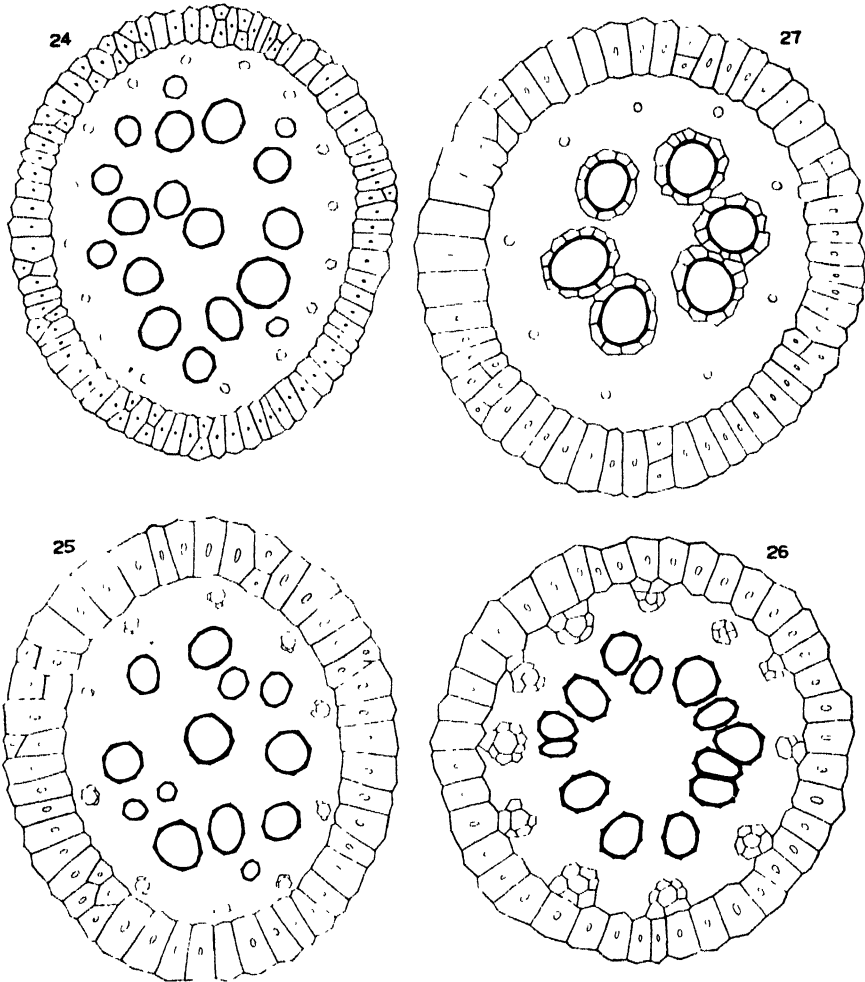
The only features of interest in the material examined are the large number of root-poles, ten to eleven, and the occurrence of an isolated metaxylem vessel in the centre of the stele. The perforations on the end-walls of the vessels are of the completely scalariform type as in *A. farinosa*. No lateral roots were available.

*ALETRIS GLABRA* Bur. et Franch. (Pratt 691).

The roots of this species have the largest steles of any examined (fig. 24). About seventeen root-poles are normally present, and the isolated metaxylem vessels are scattered throughout the stelar ground-tissue as illustrated in fig. 24.



The perforations on the end-walls of the vessels, whilst being scalariform in type, appear to differ from those of *A. farinosa* in the thinness of the transverse bars and in the relatively wide pores (figs. 16 *a*, *b*).



FIGS. 24-27.—Transverse section, steles of the main roots of *A. glabra*, *A. khasiana*, *A. languinosa*, and *A. sikkimensis*, illustrating variations in the distribution of the metaxylem. The magnification of the figure of *A. glabra* is half that of the remainder. (All except fig. 24,  $\times 300$ .)

**ALETRIS KHASIANA (Wall.) Hook. fil. (C. B. Clarke 38239).**

The roots are generally 10-arch, with a single metaxylem vessel lying in the centre of the ground-tissue (fig. 25). The perforations on the end-walls of the vessels are often definitely porose whether these are oblique or transverse.

Occasionally end-walls are found with degraded scalariform perforations (fig. 17). A similar end-wall condition is figured and described in *A. nepalensis* (infra). In the lateral roots examined the stele is triarch with two large metaxylem vessels in the centre. The endodermis is completely tertiary with fully-developed thickening (fig. 23).

*ALETRIS LANUGINOSA* Bur. et Franch. (Coll. Forrest 5653).

The roots are 10-arch, with the large metaxylem vessels forming a practically continuous ring surrounding a central ground-tissue (fig. 26). The end-walls of the large metaxylem vessels show perforations of two types—firstly, transverse end-walls with porose perforations and, secondly, oblique end-walls with degraded scalariform perforations. These latter perforations vary considerably in the extent of the degradation, sometimes only the stumps of the transverse bars remain and the perforation has become porose, whilst in others some of the transverse bars remain, but are thin, irregular, and often broken. By comparison with the results obtained with other species by the same treatment, it seems unlikely that this breaking is due to the chromic acid maceration; more probably it is due to the herbarium drying, although it may possibly be a stage in the degradation. In the lateral roots examined the stele is triarch, with two large metaxylem vessels in the centre. The endodermis is thin-walled, with the exception of the cells opposite the phloem groups which are in the advanced tertiary condition (fig. 22).

*ALETRIS NEPALENSIS* (Wall.) Hook. fil.

Material of this species was available from two different collectors:—(Capt. Lall Dhwoj (B.M.H. 0471) and Bis Ram (B.M.H. 537): these specimens agreed in anatomical characters. The roots have a relatively large parenchymatous cortex with a well-defined exodermis and papilliform surface-layer, both features being very clearly shown in material treated with caustic soda solution. The endodermis is in the mature tertiary condition. The xylem is typically 7-arch with a single ring of metaxylem vessels varying in number with the size of the root; they surround a central pith.

The end-walls of the metaxylem vessels are remarkable for the variations in structure. In the material B.M.H. 0471, some vessels had porose perforations, both oblique and transverse, one single vessel segment having a transverse porose perforation at one end and an oblique one at the other. Some of the vessels showed end-walls with degraded scalariform perforations of various types. The maximum degradation of these perforations results in the porose type, but the end-wall in this case is oblique and the margin of the pore shows the stumps of the transverse bars (fig. 18). Some of the end-walls show perforations where the irregular remnants of the transverse bars are still visible, but in none of the material examined has a degraded perforation been seen which has the transverse bars as complete as those described for *A. lanuginosa*.

The branch-roots examined are rather large. They have a papilliform epidermis, a well-marked exodermis, and a parenchymatous cortex. The endodermis is tertiary with unthickened passage-cells opposite the xylem-poles. The xylem is tetrarch with three large metaxylem vessels lying symmetrically about a central pith (fig. 20). The same branch-root cut within the tissues of the parent root shows the endodermis in the mature tertiary condition with no passage-cells, and the metaxylem vessels reduced in diameter until they are indistinguishable from the rest of the stelar ground-tissue.

ALETRIS SIKKIMENSIS Hook. fil. (G. Kiup Nat. Coll.).

The nature of the surface-layer of these roots could not be determined with any certainty, but the exodermis and parenchymatous cortex with thickened inner layer are clearly visible. The endodermis is of the heavy tertiary type and the pericycle uniformly thickened. The xylem is 9-arch, with the large metaxylem vessels in a single ring, and with a sheath of well-marked flattened ground-tissue cells round each (fig. 27). The end-walls of the metaxylem vessels have scalariform perforations of the *A. farinosa* type. Many of them are nearly transverse, and those that are oblique are quite short in length.

#### DISCUSSION.

The three features of greatest interest revealed by this investigation are (a) the nature of the surface-layer of the roots, (b) the endodermal characters, and (c) the type of perforation of the vessel segments.

There are a number of scattered reference to plants in which the roots do not develop root-hairs. Olivier (14) mentions *Crocus sativus*, *Cicuta virosa*, *Orobanchae Hederae*, *Monotropa*, *Epidendron elongatum*, and, by inference, other orchids belonging to the Epidendreae and Vandae as examples of this condition. Haberlandt (7) gives a list of marsh and water plants in which the roots are devoid of root-hairs. He notes, however, that in some plants (e.g. *Elodea canadensis*, *Nuphar luteum*, *Acorus calamus*, *Cicuta virosa*) root-hairs are absent only whilst the roots are immersed in water 'while they develop these structures in abundance on entering the soil'. Arber (1) also makes brief reference to the absence of root-hairs in *Lemna trisulca* and to the behaviour of *Elodea* in water and soil respectively.

An example of a somewhat different kind is recorded by Prillieux (16), who describes the development of root-hairs from the normally glabrous surface-layer of the aerial roots of *Vanda*, *Oncidium*, and *Aërides* on immersion in water. Root-hairs, sometimes showing digitate branching at their apices, have been noted by us in the aerial roots of a number of genera belonging to the Orchidaceae, notably in species of *Vanda* and *Laelia*, but in the examples examined by us there was no experimental interference with the mode of growth.

With regard to *Aletris farinosa* it seems clear that the absence of root-hairs is a fixed character, since they are not developed in plants grown in well-aerated soil. It has already been noted that the rounded tips of the cells constituting

the surface-layer are modified. This modification appears to be of a gelatinous nature, since particles of soil adhere firmly to the roots, much as they do to the root-hairs of most roots. It is difficult to see what biological advantage is conferred by the radial elongation of the whole of the piliferous layer, since the increase in the area of the absorbing surface must be relatively small.

An examination of the roots of members of the related subfamily Mondoideae (10) shows that the majority of these possess normal root-hairs. In *Liriope spicata*, however, they were absent in our material, although the cells of the surface-layer were not elongated as they are in *Aletris*.

The endodermis of *Aletris* is interesting both on account of the prosenchyma-like character of the individual cells and also because of the small number of 'passage cells' and the rapid assumption by these of the tertiary condition. Kroemer (11) mentions a number of somewhat similar instances and notes that, as a rule, the attainment of a completely tertiary endodermis is followed by the death of the root cortex, though this is not invariably the case.

The scalariform nature of the perforation of the vessel segments in *A. farinosa* and *A. aurea* appears, as has been previously stated, to be the first record of such a condition among Monocotyledons.

Among Dicotyledons this condition has been known to exist in the Betulaceae and Ericaceae since the middle of last century (6)\*. More recently the work of Prof. E. C. Jeffrey and his associates (4, 12, 17) has increased our knowledge of such types, and this school of plant anatomists regards the scalariform grids across the ends of the vessel segments as a more primitive condition than that in which open pores exist. Jeffrey (9) figures examples of widely-spaced bars in *Liriodendron*, and examples of progressive degradation leading to the open pore condition in *Vaccinium corymbosum*, and many other examples are known. Whilst the herbarium material of the various Asiatic species of *Aletris* used by us is not ideal for work of this kind, it seems evident that within the limits of the genus a complete series of transitions from the fully scalariform perforation to the open pore may be found. It is possible that a more intensive study of other Monocotyledons will reveal further examples of a similar nature, but it would obviously be absurd to initiate a discussion on its possible evolutionary significance on the strength of its occurrence in *Aletris* alone.

#### SUMMARY.

(1) *Aletris* is a liliaceous genus with both American and Asiatic species, all of which possess a rhizome bearing tough, wiry, adventitious roots.

(2) The roots are characterized by the peculiar nature of the surface-layer, all the cells being elongated radially and forming a closely-set system of papillae.

\* Sanio's paper, 'Vergleichende Untersuchungen über die Elementarorgane des Holzkörpers' (Sanio, C., Bot. Zeit. Jahrg. 21, 1863) forms the basis of all the later work on vessel connections.

(3) The root endodermis is composed of elongated cells with pointed ends similar to prosenchymatous fibres. These develop extremely heavy thickenings of lignocellulose.

(4) There are a few isolated passage-cells in the young root, but they develop the tertiary condition a short distance behind the root-tip.

(5) In old roots all the tissues external to the endodermis are frequently exfoliated.

(6) The metaxylem vessels in *Aletis farinosa* possess scalariform perforations between the vessel segments.

(7) There is evidence that in the various species of *Aletis* there is a series of transitional stages from the scalariform perforation to the ring type.

(8) An examination of herbarium material suggests that the root anatomy may be of value in differentiating between the various species.

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Acknowledgments are also due to the Department of Scientific and Industrial Research for a maintenance allowance to the junior author for purposes of research training.

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The genus *Potamogeton* L. in Tropical Africa.

By J. E. DANDY, M.A., F.L.S.

(PLATES 21 &amp; 22 and 9 Text-figures)

[Read 4 March 1937]

THE need for a revision of *Potamogeton* as represented in 'Tropical Africa' \* has been apparent for some time to students of the aquatic flora of the region. In 1901 this notoriously difficult genus was worked out in the 'Flora of Tropical Africa' by A. Bennett † from the limited material at his disposal, but since that date no treatment has appeared which deals fully and exclusively with the Tropical African species, though the genus has been included in various regional lists and floras such as A. Peter's 'Flora von Deutsch-Ostafrika' ‡ and Hutchinson and Dalziel's 'Flora of West Tropical Africa' §. It is true that in 1907 *Potamogeton* was monographed in 'Das Pflanzenreich' by Graebner ||, but as regards Tropical Africa he was content to accept Bennett's treatment with very slight modification, and thus added little to our knowledge of the forms occurring there. In 1916 appeared Hagström's account of the *Potamogetons* collected by R. E. Fries on the Swedish Rhodesia-Congo Expedition of 1911-12 ¶, and this was quickly followed by the same author's monumental study of the genus *Potamogeton* which was published under the title 'Critical Researches on the *Potamogetons*' \*\*. The latter work, though comprehensive in character, not unnaturally deals at greatest length with the European species, and especially with the Scandinavian forms which Hagström knew so well thanks to a wealth of herbarium specimens supplemented by careful observation in the field. It contains detailed accounts of the widespread species which are represented in Tropical Africa, but unfortunately Hagström,

\* For the purpose of this paper the Cape Verde Islands and the island of Socotra are included in Tropical Africa.

† A. Bennett, 'Potamogeton', in Dyer, Fl. Trop. Afr. viii, 219-224 (1901).

‡ A. Peter, 'Potamogeton', in Fedde, Repert. Sp. Nov., Beih. xl, 1, 112-113 (1929).

§ J. Hutchinson, 'Potamogeton', in Hutch. & Dalziel, Fl. W. Trop. Afr. ii, 307 (1936).

|| P. Graebner, 'Potamogeton', in Engl. Pflanzenr. iv, 11, 39-142, figs. 13-29 (1907).

¶ J. O. Hagström, 'Potamogetonaceæ', apud R. E. Fr. in Wiss. Ergebn. Schwed. Rhodes.-Kongo-Exped. i, 185-188, figs. 15-16 (1916).

\*\* In K. Svensk. Vetenskapsakad. Handl., Ny Följd, lv, 5, 1-281, figs. 1-119 (1916). For the sake of brevity this work is cited as 'Crit. Res.' throughout the present paper.

working in Sweden, had access to very few Tropical African specimens. In the whole of the work only fourteen Tropical African gatherings are mentioned, and apparently he saw no authentic material at all of Bennett's species *P. Livingstonei* and *P. Schweinfurthii*. Thus Hagström's knowledge of the Tropical African forms was far from complete, and this circumstance, coupled with his over-reliance on purely anatomical characters of stem and leaf, led to his distinguishing two new species based on sterile specimens which he would probably have identified with known species had a better range of Tropical African material been available for comparison. Bennett's treatment of *Potamogeton* in the 'Flora of Tropical Africa' was based, according to his citations, on a total of forty-one Tropical African gatherings\* together with records from the literature. Recent botanical explorations in Tropical Africa, and particularly in the eastern region of mountains and lakes, have produced an extensive series of specimens of *Potamogeton*, and having examined more than 160 gatherings, mostly in the British Museum and Kew Herbaria, I feel justified in offering the present revision.

#### NUMBER OF SPECIES.

Despite the range of material now available, the taxonomy and geography of *Potamogeton* in Tropical Africa cannot yet be worked out in such great detail as in the *Potamogetons* of Europe and North America, where the forms have been more or less exhaustively studied both in the herbarium and in the field. As far as I can ascertain, no special field-work has been carried out with regard to *Potamogeton* in Tropical Africa, and gaps in the known distribution of some of the species, notably *P. trichoides* and *P. crispus*, suggest that careful search may discover them in many more localities. The taxonomic problem, however, is simpler than in the North Temperate countries, since the number of species represented in Tropical Africa is few and there is as yet no evidence of the facile hybridization that complicates matters in regions which are strongholds of the genus.

In the 'Flora of Tropical Africa' Bennett recognized twelve species in Tropical Africa: he sorted his limited material (forty-one gatherings, as remarked above) into eleven species, and added a twelfth, *P. coloratus*, on the slender evidence of a record of *P. plantagineus* published by Engler in an account of the vegetation of East Africa. When, however, Bennett's twelve 'species' are studied in conjunction with the additional material which has since become available, they are found to be reducible to six valid species, as indicated briefly in the following table wherein the ordinal numbers are those used in the 'Flora of Tropical Africa':—

\* Actually forty-three gatherings were cited, but one of these belongs to *Ruppia* (see p. 516, under *P. pectinatus*) and another is not from Tropical Africa (see p. 538, under *P. crispus*).





Kenya and Uganda. A further addition to the Tropical African species is a plant from Ahaggar, just south of the Tropic of Cancer, collected in a sterile condition in 1928 by Maire, who referred it to *P. pusillus*; this plant appears to be specifically distinct from any other known form, and I therefore describe it as new under the name *P. hoggarensis*. With these three species the total number of species of *Potamogeton* known from Tropical Africa is brought up to nine.

#### GEOGRAPHICAL DISTRIBUTION OF THE SPECIES.

*Potamogeton* is essentially a Temperate genus, and it is not surprising, therefore, that the species found in Tropical Africa are few and are mostly confined to the more elevated regions. The only endemic species is *P. hoggarensis* (fig. 4), and even this may occur outside the area of Tropical Africa, for it is known from but a single locality in Ahaggar, in the central Sahara just south of the Tropic of Cancer, and may possibly extend north of the Tropic. *P. hoggarensis* cannot be regarded as belonging to the Tropical African flora proper, and the same remark applies to *P. perfoliatus* (fig. 8), a species of circumboreal distribution which extends southwards from North Africa into the high mountain masses of the central and eastern Sahara just south of the Tropic of Cancer. (Recently *P. perfoliatus* has been collected in a canal in the Blue Nile Province of the Anglo-Egyptian Sudan, but the species is probably adventive here.) At the other extreme, phytogeographically, is *P. octandrus* (fig. 2), a species widely dispersed in the Tropics and Subtropics of the Old World; it has a scattered distribution in Tropical and north-eastern South Africa, and is the only genuine Tropical element among the Potamogetons of Tropical Africa. The remaining six species are concentrated in the mountain and lake region of East Africa, though some of them have westward extensions in the north and south, and all of them extend into South Africa. Their general distribution is, in fact, of a type characteristic of North Temperate elements in the Tropical African flora. *P. trichoides* (fig. 3) is a species of wide distribution in western and central Europe, extending to Kashmir, western North Africa, and through East Africa to Cape Province; in Tropical Africa it has been collected in Kenya, Uganda, and Southern Rhodesia. *P. panormitanus* (fig. 5), a species which has been much confused with *P. pusillus*, is widely dispersed in Europe, North Africa, Temperate Asia, and North America; it occurs in the Cape Verde Islands, and from North Africa it extends southwards into the Sahara and through East Africa to the Cape. *P. pectinatus* (fig. 1), the most widespread of all Potamogetons, is the only African representative of the section *Coleophylli*; it has been collected in numerous localities in East Africa, including the island of Socotra, and has also been recorded from southern Angola and South West Africa. *P. nodosus* (fig. 7), like *P. pectinatus*, is represented by numerous gatherings from East Africa, including Socotra, and in the south extends westwards to Angola. It has also been collected at the mouth of the Congo and in the massif of Tibesti in the eastern Sahara,

*P. nodosus* is a widespread species in the warmer parts of both Hemispheres. *P. Schweinfurthii* (fig. 6), which may be regarded as the African equivalent of *P. lucens*, has a wide distribution in eastern Africa from Lower Egypt southwards to Cape Province; in addition, it occurs in north-western Africa from Tunisia to Senegal, and in Tropical South West Africa. *P. crispus* (fig. 9), a widespread plant in the Old World, ranges from Egypt southwards through East Africa to Cape Province; I have seen specimens from the Anglo-Egyptian Sudan, Nyasaland, and Southern Rhodesia, and there is a record of its occurrence in Abyssinia.

#### SOUTH AFRICAN MATERIAL.

With the exceptions of *P. hoggarensis* and *P. perfoliatus*, all the Tropical African species of *Potamogeton* extend into Temperate South Africa, and for each I have studied South African material along with that from Tropical Africa. No attempt is made in the present paper to deal with all the forms recorded from South Africa, but the opportunity is taken to cite, in a footnote under each Tropical African species, some of the South African material which I have examined. The following species, based on South African specimens, are reduced :—

<i>P. Thunbergii</i> Cham. & Schlecht. (1827)	to <i>P. nodosus</i> Poir. (1816).
<i>P. badius</i> Hagstr. (1916)	to <i>P. panormitanus</i> Biv. (1838).
<i>P. capensis</i> Scheele ex Hagstr. (1916)	} to <i>P. Schweinfurthii</i> A. Benn. (1901).
<i>P. promontoricus</i> Hagstr. (1916)	
<i>P. venosus</i> A. Benn. (1924)	

#### LOCATION OF SPECIMENS EXAMINED.

The work of preparing this revision has been carried out in the Department of Botany, British Museum (Natural History), and all the material there has been examined and compared with the collection in the herbarium of the Royal Botanic Gardens, Kew. In addition, I have seen important specimens kindly loaned by the authorities of the other institutions listed below, to whom my thanks are due.

In the ensuing enumeration of the species abbreviations are used to indicate the herbaria in which the specimens seen are preserved; these are as follows :—

Alg	=	Herbier général de l'Université, Alger.
AM	=	Albany Museum, Grahamstown.
BM	=	British Museum (Natural History).
Coi	=	Instituto Botanico, Coimbra.
E	=	Royal Botanic Garden, Edinburgh.
HLT	=	Herbier G. Le Testu.
K	=	Royal Botanic Gardens, Kew.
NHP	=	National Herbarium, Pretoria.
SAM	=	South African Museum, Cape Town.
Up	=	Universitetets Botaniska Museum, Uppsala.

*Key to the species.*

- Stipules adnate to the lower part of the leaf, forming a basal leaf-sheath; leaves narrowly linear to setaceous, entire, all submersed (Sect. I. COLLOPHYLLI) ..... 1. *P. pectinatus*.
- Stipules free or almost free from the leaf, forming an independent stipular sheath which is sometimes caducous or fugacious:
- Fruiting-carpels short-beaked (the beak much less than half as long as the body of the carpel), with or without a dorsal tooth near the base; stems terete or somewhat compressed; leaves entire or minutely denticulate:
- Submersed leaves under 3 mm. in breadth and with 3-5 nerves (though sometimes appearing only 1-nerved owing to the faintness of the lateral nerves), narrowly linear to filiform, sessile, entire; spikes under 2 cm. long, with few or comparatively few flowers; floating leaf-laminas (if present) usually less than 3.5 cm. long and 1 cm. broad (Sect. II. CHLOEPHYLLI):
- Stipular sheaths open and convolute; fruiting-carpels (unknown in *P. hoggarensis*) about 2-3 mm. long, smooth or more or less muriculate on the back:
- Plant with or without coriaceous floating leaves; submersed leaves with a well marked lacunar system bordering the midrib and usually extending sideways to the lateral nerves; stipular sheaths caducous; floating leaves (if present) petiolate, with a more or less expanded lamina; carpels normally 4 (but sometimes reduced to 3 or 2) in each flower ..... 2. *P. octandrus*
- Plant without coriaceous floating leaves; leaves without a lacunar system or with a narrow lacunar system bordering the midrib but not extending sideways to the lateral nerves; stipular sheaths subsistent:
- Leaves mostly under 1 mm. in breadth, 3-nerved but usually appearing only 1-nerved owing to the faintness of the 2 lateral nerves; stipular sheaths mostly under 2 cm. long; carpels usually reduced to 1 in each flower ..... 3. *P. trichoides*.
- Leaves up to about 2.5 mm. in breadth, 3-5-nerved; stipular sheaths up to about 2-3 cm. long at maturity ..... 4. *P. hoggarensis*.
- Stipular sheaths closed and tubular at least when young; fruiting-carpels about 1.5-2.8 mm. long, smooth; plant without coriaceous floating leaves; leaves up to about 3 mm. in breadth, 3-5-nerved, without a well marked lacunar system bordering the midrib (except sometimes in the uppermost or 'involucral' leaves) ..... 5. *P. panormitanus*
- Submersed leaves (if present) mostly well over 3 mm. in breadth and with 7 or more nerves, linear or broader in shape, sessile or more or less petiolate, entire or minutely denticulate; spikes often over 2 cm. long, with numerous or comparatively numerous flowers; floating leaf-laminas (if present) mostly more than 3.5 cm. long and 1 cm. broad (Sect. III. HETEROPHYLLI);

Leaves subsessile or more or less petiolate, not amplexicaul :

Leaves all or mostly submersed (the upper ones sometimes floating) ; submersed leaves subsessile or with a more or less elongated petiole, linear to lanceolate or narrowly elliptic-oblong ; floating leaves (if present) with a more or less elongated petiole, the lamina lanceolate to oblong or narrowly elliptic-oblong with a cuneate to rounded base ; fruiting-carpels about 3-4 mm. long . . . . .

6. *P. Schweinfurthii*.

Leaves (in mature plants) all or mostly floating (the lower ones submersed but often disappearing early), all with a more or less elongated petiole ; lamina of floating leaves lanceolate to elliptic or oblong or ovate-oblong with a cuneate to rounded or subcordate base ; fruiting-carpels about 2.5-5.5 mm. long . . . . .

7. *P. nodosus*.

Leaves mostly sessile, amplexicaul, suborbicular or ovate to lanceolate or elliptic-oblong, all submersed . . . . .

8. *P. perfoliatus*.

Fruiting-carpels long-beaked (the beak from half to wholly as long as the body of the carpel), with a more or less prominent dorsal tooth near the base ; stems compressed ; leaves serrulate, sessile, narrowly oblong to linear, 3-5-nerved, up to about 15 mm. in breadth, usually more or less crisped, all submersed ; spikes with few or comparatively few flowers (Sect. IV. BATRACHOSERIS) . . . . .

9. *P. crispus*.

#### Sect. I. COLEOPHYLLI Koch.

1. *POTAMOGETON PECTINATUS* L. Sp. Pl. i, 127 (1753). A. Rich. Tent. Fl. Abyssin. ii, 354 (1851). Garcke in Peters, Naturwiss. Reis. Mossamb., Bot. 511 (1864). Aschers. & Schweinf. in Schweinf. Beitr. Fl. Aethiop. i, 292 (1867). A. Benn. apud Balf. f. in Trans. R. Soc. Edin. xxxi, 300 (1888) ; in Journ. of Bot. xxxiii, 138 (1895) ; in Dyer, Fl. Trop. Afr. viii, 223 (1901), pro parte ; apud Rendle in Journ. Linn. Soc., Bot. xxxviii, 23 (1907). Dur. & Schinz, Consp. Fl. Afr. v, 495 (1894). Schweinf. in Bull. Herb. Boiss. ii, App. 2, 92 (1894). K. Schum. in Engl. Pflanzenw. Ost-Afr. C, 93 (1895). Schinz in Bull. Herb. Boiss. iv, App. 3, 9 (1896). Rendle in Cat. Afr. Pl. Welw. ii, 94 (1899). Graebn. in Engl. Pflanzenr. iv, 11, 121, fig. 28 A-B (1907), pro parte ; apud Mildbr. in Wiss. Ergebn. Deutsch. Z.-Afr. Exped. ii, 42 (1910). Engl. in Engl. & Drude, Veg. Erd. IX, ii, 95 (1908). Hagstr. apud R. E. Fr. in Wiss. Ergebn. Schwed. Rhodes.-Kongo-Exped. i, 188 (1916) ; Crit. Res. 39, figs. 15-18 (1916), pro parte. De Wild. Pl. Bequaert. i, 8 (1921). Dinter in Fedde, Repert. Sp. Nov. xxii, 383 (1926). A. Peter in Abhandl. Ges. Wiss. Götting., Math.-Phys. Kl., Neu. Folg. xiii, 2, 108 (1928) ; in Fedde, op. cit., Beih. xl, 1, 113 (1929). Robyns in Ann. Soc. Sci. Brux., sér. B, iv, 305 (1935). Dandy apud Jenkin in Ann. & Mag. Nat. Hist., ser. 10, xviii, 177 (1936).

*Potamogeton interruptus* Kit. in Schult. Österr. Fl., ed. 2, i, 328 (1814).

*Potamogeton pectinatus* var. *scoparius* Wallr. Sched. Crit. i, 68 (1822).

*Potamogeton zosteraceus* Fr. Novit. Fl. Suec., ed. 2, 51 (1828).

*Potamogeton filiformis* (non Pers.).—A. Benn. in Dyer, loc. cit. (1901). Graebn. in Engl. Pflanzenr. iv, 11, 126 (1907), pro parte. Engl. in Engl. & Drude,

loc. cit. (1908). A. Peter in Abhandl. Ges. Wiss. Götting., Math.-Phys. Kl., Neu. Folg. xiii, 2, 107 (1928); in Fedde, loc. cit. (1929).

*Potamogeton Livingstonei* A. Benn. loc. cit. (1901); apud Rendle in Journ. Linn. Soc., Bot. xxxviii, 23 (1907). Graebn. tom. cit. 127 (1907). Engl. loc. cit. (1908). Hagstr. op. cit. 53 in obs. (1916).

*Potamogeton pectinatus* proles *interruptus* (Kit.) Graebn. tom. cit. 124 (1907).

*Potamogeton pectinatus* proles *scoparius* (Wallr.) Graebn. tom. cit. 125, fig. 28 G (1907).

*Potamogeton pectinatus* proles *zosteraceus* (Fr.) Graebn. tom. cit. 126 (1907).

SOCOTRA. 1880, I. B. Balfour 152 (or 650) (E, sterile).

ANGLO-EGYPTIAN SUDAN. Blue Nile Prov.: Gezira canals, 1936, F. W. Andrews W12 (BM; K).

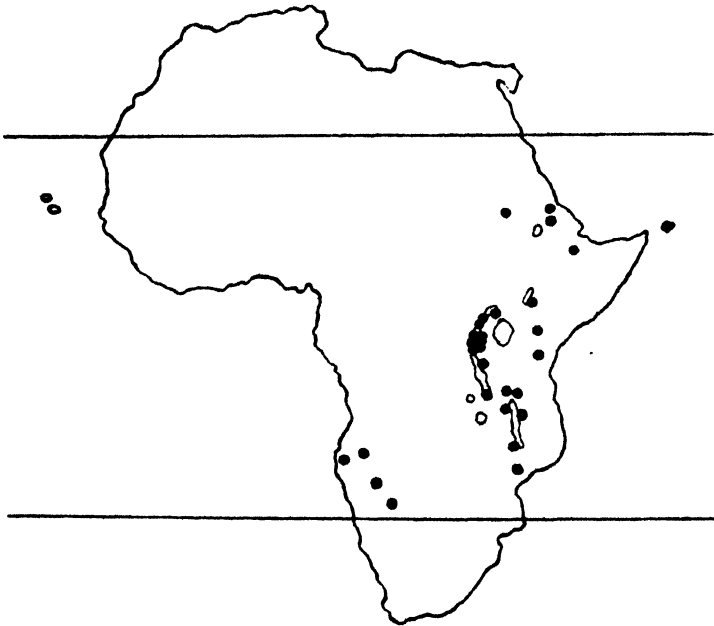


FIG. 1.—Distribution in Tropical Africa of *Potamogeton pectinatus* L.

ERITREA. Adi Ugri region, near Godofelassi, 1,950 m., 1894, G. A. Schweinfurth & D. Riva 138 (ex Schweinfurth).

ABYSSINIA. Haramaia, 9° 24' N., 42° E., c. 2,000 m., 1933, J. B. Gillett 5467 (BM; K).

KENYA. Northern Frontier Prov.: East shore of L. Rudolf, 1931, E. B. Worthington (BM, sterile). East shore of L. Rudolf, opposite Central Island, 1931, E. B. Worthington 290.3 (BM, sterile). Naivasha Prov.: L. Naivasha, 1929, P. M. Jenkin (BM, sterile).

UGANDA. Northern Prov.: Bunyoro Distr., L. Albert, near Butiaba, 1912, R. E. Fries 2000 (Up, sterile). Western Prov.: Toro Distr., near Fort Portal,

Nyakasura, 1934, *G. Taylor* 2336 (BM). Toro Distr., Ruwenzori, 1893-94, *G. F. Scott Elliot* (BM; K). Kigezi Distr., L. Bunyonyi, c. 2,000 m., 1933, *A. S. Thomas* 1210 (K). Kigezi Distr., L. Bunyonyi, 1931, *E. B. Worthington* 711 in part (BM, sterile) and without no. (BM, sterile).

BELGIAN CONGO. Kivu Distr.: Southern bank of L. Edward, Kabare, 1914, *J. Bequaert* 5312 (K). Southern end of L. Edward, 1912, *R. E. Fries* 1742 (Up). L. Kivu, Kwijiwi I., 1911, *R. E. Fries* 1582 (Up). Ruanda Distr.: L. Kivu, Kisenyi, 1927, *D. H. Linder* 2019a (K). L. Kivu, between Kisenyi and Sake, Kesheru, 1931, *B. D. Burtt* 3267 (K). L. Kivu, Shangugu, 1927, *D. H. Linder* 2019 (K).

TANGANYIKA TERRITORY. Iringa Prov.: Rungwe Distr., Rungwe, R. Kibira, 1,400 m., 1913, *A. Stolz* 2253 (BM; K; NHP). Rungwe Distr., Kigala, R. Kibila, 1,400 m., 1914, *A. Stolz* 2649 (BM; K; NHP). Lindi Prov.: Songea Distr., L. Nyasa, Lukoma, 1887, *W. Bellingham* (BM, sterile, syntype of *P. Livingstonei*).

NYASALAND. Northern Prov.: North Nyasa Distr., L. Nyasa, Kambwe Lagoon, 1877, *Laus* 3 (BM, sterile, syntype of *P. Livingstonei*; K, sterile, syntype of *P. Livingstonei*); 1904, *W. A. Cunningham* 12 (BM, sterile). Northern Prov. or Southern Prov.: West shore of L. Nyasa, south-western bay, 1861, *J. Kirk* (K, syntype of *P. Livingstonei*).

PORTUGUESE EAST AFRICA. Companhia Moçambique: Rios de Sena, Chupanga, *W. C. H. Peters* (ex Garcke).

NORTHERN RHODESIA. Tanganyika Prov.: L. Tanganyika, Mtondwe Bay, 1904, *W. A. Cunningham* 23 (BM).

ANGOLA. Mossamedes Distr.: Near Aguadas, 1859, *F. Welwitsch* 250 (BM, sterile; Coi, sterile; K, sterile).

SOUTH WEST AFRICA. Herero country: Gross Huis, 1934, *E. B. W. Schoenfelder* 1008 (NHP). Western edge of Kalahari, Oas, 1886, *H. Schinz* 780 (AM; Coi).

This is the most widely spread species of *Potamogeton*, its distribution, according to Hagström (Crit. Res. 44), 'being universal and surpassing all the other species of the genus'. It was originally described from Europe.

*P. pectinatus* is the only African representative of the section *Coleophylli*. In Tropical Africa it is well distributed in the mountain and lake region of the east, while in the south it extends westwards to southern Angola and South West Africa\*. It also occurs in the island of Socotra. In the 'Flora of Tropical

\* Further south it occurs in South Africa. I have seen the following specimens:—TRANSVAAL: *J. Burt Davy* 2534 (NHP 19); *J. G. Gilmore* 2113 (NHP); *L. C. C. Liebenberg* 2456 (NHP); *C. E. Moss* 16293 (BM); *W. Nelson* 225 (K); *F. Wilms* 1654 (BM). NATAL: *R. Schlechter* 2969 (AM, sterile; BM, sterile; K, sterile; NHP, sterile); *J. Wylie* in *Herb. J. Medley Wood* 8476 (SAM 23672). ORANGE FREE STATE: *J. W. Pont* 599 (NHP); without collector (NHP 15, sterile). CAPE PROVINCE: *C. F. Ecklon & C. L. P. Zeyher* 644 (BM; K; SAM 4523); *F. H. Holland* 612 (AM) and without no. (AM); *C. E. Moss* 5658 (AM) and 7881 (AM); *A. Pegler* 438 (NHP); *G. Rattray* 869 (AM); *R. Schlechter* 9592 (AM; BM; Coi; K; NHP); *F. W. Turpin* (SAM 4431); *A. H. Wolley Dod* 3643 (BM; K).

Africa ' the species was recorded from Upper Guinea, but the material concerned—a specimen collected in the Gold Coast by G. Don—is referable to *Ruppia maritima* L.\*

There are a great many forms of *P. pectinatus*, with (relatively) thick or slender stems, broad or narrow leaves, long or short leaf-sheaths, and large or small fruits. Tropical African specimens show considerable variation in the vegetative characters, particularly in the breadth of the leaves, and this fact apparently influenced A. Bennett so much that in the 'Flora of Tropical Africa' he separated the limited material available (seven or eight gatherings all told) into three groups which he treated as specifically distinct. The first he called *P. pectinatus*; the second he referred to *P. filiformis* Pers.; the third he described as new under the name *P. Livingstonei*.

The material referred by Bennett to *P. filiformis* was collected by Scott Elliot on his Ruwenzori Expedition. It is a form of *P. pectinatus* with narrow leaves and slender spikes, flowering but lacking fruit. Certainly it is not the true *P. filiformis* which is an exclusively North Temperate species unknown from Africa. Graebner in 'Das Pflanzenreich' (p. 126) accepted Bennett's identification of the Ruwenzori plant and added a doubtful record of *P. filiformis* from Socotra based on a Balfour plant which is *P. pectinatus*. More recently *P. filiformis* has been recorded from Tanganyika Territory by A. Peter on the basis of sterile material collected by himself (no. 46199) in Lake Tanganyika near Ujiji, Kigoma District. I have not seen his plant, but it is presumably a form similar to that gathered by Scott Elliot.

*P. Livingstonei* was based on three gatherings from Lake Nyasa, collected by Kirk, Laws (no. 3), and Bellingham. In a note following the description it was stated to be 'A remarkable species, combining the habit of *P. Robbinsii*, Oakes and *P. pectinatum*, Linn., but with the basal portion quite like a *Cymodocea*, in texture and rigidity'. Kirk's specimen (in Herb. Kew.) has flowering spikes but no fruit, and is a rather broad-leaved example of *P. pectinatus* resembling some European forms to which such names as *P. interruptus* Kit. and *P. flabellatus* Bab. have been given. Laws's gathering, which is represented in both the British Museum and Kew Herbaria, consists of sterile material with leaves still broader (up to about 2–3 mm. in width) though not as broad as those seen in some extra-African forms of *P. pectinatus* such as the one named *P. zosteraceus* by Fries. Bellingham's specimen, at the British Museum, is a sterile example similar to Laws's plant. In 1895, six years before he published in the 'Flora of Tropical Africa', Bennett (in Journ. of Bot. xxxiii, 139) had remarked: 'there is a species in Lake Nyassa allied to *P. Robbinsii* Oakes, of N. America; whether it is that species or a new species, the fragmentary specimens seen are quite insufficient to decide'. A manuscript note to the same effect, dated 1897, was affixed by him to Laws's specimen in the British Museum Herbarium, and it is therefore evident that in separating *P. Livingstonei* from *P. pectinatus*

\* See footnote under *P. panormitanus* (p. 525).



Bennett was unduly influenced by the broad-leaved sterile specimens of Laws and Bellingham. Now, as mentioned above, *P. pectinatus* is particularly variable in the breadth of the leaves, and there is often considerable difference in leaf-breadth even on the same individual plant. Hagström (Crit. Res. 41) observed: 'Concerning the leaf-width it may be remarked that the leaves of the main-shoot are always broader than the branch-leaves, and the lower leaves of a shoot also broader than the upper ones'. Thus it seems that Bennett's 'remarkable species' was based primarily on sterile specimens of *P. pectinatus* with the broad (lower) type of leaf. Graebner in 'Das Pflanzenreich' (p. 127) retained *P. Livingstonei* and under it cited Laws ('Lawson') no. 3, but it is significant that in his list of collectors' numbers (p. 164) he cited Dickie no. 3 (which is the same gathering! \*) as '*P. pectinatus* (f. *latifolia*)'. Finally, it may be mentioned that Hagström did not see *P. Livingstonei*; he merely speculated as to its affinity (Crit. Res. 53).

## Sect. II. CHLOEPHYLLI Koch.

2. POTAMOGETON OCTANDRUS Poir. in Encycl. Méth., Bot., Suppl. iv, 534 (1816). Hutch. in Hutch. & Dalziel, Fl. W. Trop. Afr. ii, 307 (1936).

*Hydrogeton heterophyllum* Lour. Fl. Cochinch. i, 244 (1790)—non *Potamogeton heterophyllum* Schreb. (1771).

*Potamogeton javanicus* Hassk. in Act. Soc. Sci. Ind.-Neêrl. i, 8, 26 (1856). Schinz in Ber. Schweiz. Bot. Ges. i, 60 (1891); in Bull. Herb. Boiss. iv, App. 3, 9 (1896). A. Benn. in Journ. of Bot. xxix, 121, 186 (1891); op. cit. xxxiii, 138 (1895); in Ann. K. K. Naturhist. Hofmus. Wien, vii, 288 (1892); in Dyer, Fl. Trop. Afr. viii, 220 (1901); in Annu. Conserv. & Jard. Bot. Genève. ix, 100 (1905); apud Rendle in Journ. Linn. Soc., Bot. xxxviii, 24 (1907). Dur. & Schinz, Consp. Fl. Afr. v, 495 (1894). K. Schum. in Engl. Pflanzenw. Ost-Afr. C, 93 (1895); in Warb. Kunene-Sambesi Exped. Baum, 171 (1903). Rendle in Cat. Afr. Pl. Welw. ii, 94 (1899). Graebn. in Engl. Pflanzenr. iv, 11, 46, fig. 14 A-C (1907). Engl. in Engl. & Drude, Veg. Erd. IX, ii, 95 (1908). Thonner, Blütenpfl. Afr. t. 4 (1908); Flow. Pl. Afr. t. 4 (1915). Hagstr. apud R. E. Fr. in Wiss. Ergebn. Schwed. Rhodes-Kongo-Exped. i, 185 (1916); Crit. Res. 131, fig. 58 (1916). A. Peter in Abhandl. Ges. Wiss. Götting., Math.-Phys. Kl., Neu. Folg. xiii, 2, 108 (1928); in Fedde, Repert. Sp. Nov., Beih. xl, 1, 113 (1929). Broun & Massey, Fl. Sudan, 367 (1929). Bremek. & Oberm. in Ann. Transv. Mus. xvi, 401 (1935).

*Potamogeton huillensis* Welw. ex Schinz in Ber. Schweiz. Bot. Ges. i, 61 (1891), *nomen synonymum*.

*Potamogeton Preussii* A. Benn. in Dyer, tom. cit. 222 (1901), pro parte, quoad pl. ex Cameroons; in Annu. Conserv. & Jard. Bot. Genève. ix, 100 (1905). Graebn. tom. cit. 106 (1907), pro parte. Engl. loc. cit. (1908), pro parte. Hagstr. op. cit. 114, fig. 50 (1916).

\* According to the label on the Kew specimen Laws's no. 3 was communicated by Dickie.

*Potamogeton* near *pectinatum*, Linn.—Broun, Cat. Sudan Flow. Pl. 86 (1906).

*Potamogeton javanicus* var. *major* A. Benn. ex Graebn. tom. cit. 161 (1907),  
pro parte, quoad pl. africanam.

*Potamogeton*.—A. Chev. Sudania, i, 126, no. 7856 (1911).

NIGERIA. Northern Provinces : Nupe Distr., near Jeba, 1857, *C. Barter* 1069 (K). Southern Provinces : Cameroons South Distr., Kumba (Barombi), Elephant Lake, near Barombi-ba-Mbu, 1890, *P. Preuss* 451 (BM, syntype of *P. Preussii*). Cameroons South Distr., Kumba (Johann-Albrechtshöhe), bank of Elephant Lake, 220 m., 1895, *A. Staudt* 462 (BM, sterile, syntype of *P. Preussii*).

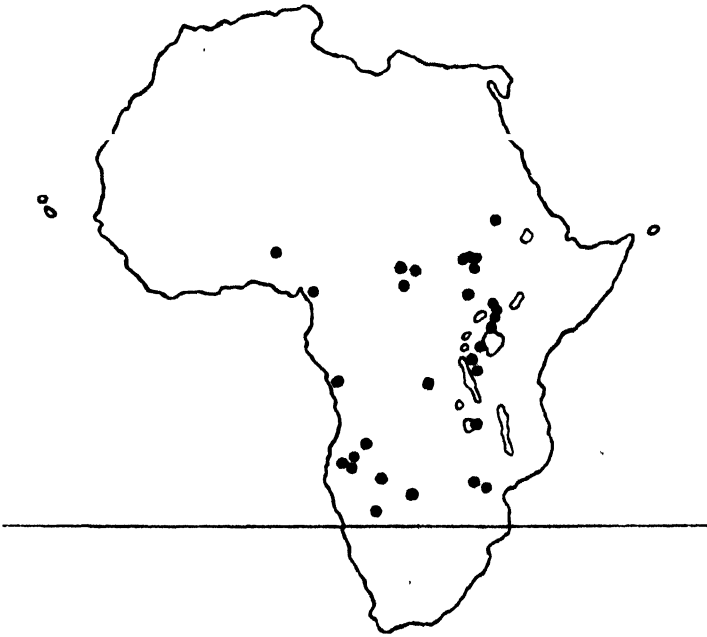


FIG. 2.—Distribution in Tropical Africa of *Potamogeton octandrus* Poir.

FRENCH EQUATORIAL AFRICA. Oubangui-Chari : Eastern Chari (Snoussi country), L. Ni, 1903, *A. Chevalier* 7856 (K, sterile). 70 Km. south of Ouadda, Doumendé, R. Dinga (affluent of R. Koto), 1921, *G. Le Testu* 3457 (BM ; HLT). Haute-Bangui, 100 Km. north-east of Alindao, R. Wakpire, 1924, *C. Tisserant* 1420 (BM ; HLT).

ANGLO-EGYPTIAN SUDAN. Upper Nile Prov. : Bahr el Ghazal, downstream from Wad Jarkh, 1930, *N. D. Simpson* 7701 (BM ; K). Bahr el Jebel, Sudd, 1903, *A. F. & H. M. Broun* (K). Bahr el Jebel, Adok Causeway, 1929, *N. D. Simpson* 7183 (BM, sterile ; K, sterile). Equatorial Prov. : Bahr el Ghazal, mouth of Bahr el Arab, 1869, *G. A. Schweinfurth* 1225 (E ; K). Zande (Niam-niam) country, R. Rei, near Gumango hill, 1870, *G. A. Schweinfurth* 2909 (K).

UGANDA. Northern Prov.: Gulu Distr., Keyo County, near Lamogi, 1935, *W. J. Eggeling* E.1655 (BM). Bunyoro Distr., Victoria Nile, Mutunda, 1935, *W. J. Eggeling* E.2227 (BM). Bunyoro Distr., Victoria Nile above Masindi Port, 1935, *G. Taylor* 3326 (BM). Buganda Prov.: Entebbe Distr., L. Victoria, Entebbe, 1905, *A. G. Bagshawe* 703 (BM); 1929, *L. C. C. Liebenberg* 734 (K).

BELGIAN CONGO. Urundi Distr.: Between R. Malagarasi and Mgoni, *A. Peter* 37963 (ex *A. Peter* under *P. javanicus*). Katanga Prov.: Lomami Distr., between R. Lubilash and R. Lomami, Bena Ki, 1882, *P. Pogge* 1506 (ex Graebner under *P. javanicus*).

TANGANYIKA TERRITORY. Lake Prov.: Bukoba Distr., L. Victoria, Bukoba, 1905, *W. A. Cunningham* 54 (BM).

NORTHERN RHODESIA. Awemba Prov.: L. Bangweulu, Chirui I., near Mwanamburo, 1911, *R. E. Fries* 1024 (K; Up).

SOUTHERN RHODESIA. Mashonaland: Salisbury Distr., Cleveland Dam, c. 1,500 m., 1917, *F. Eyles* 655 (BM). Salisbury Distr., Cleveland Dam, 1927, *M. E. Blenckiron* in *Herb. C. E. Moss* 14860 (BM). Makoni Distr., R. Odzi, c. 900 m., 1928, *F. Eyles* 5853 (K). Southern Rhodesia, without locality: *A. Hislop* Z.108 (K, sterile).

ANGOLA. Zaire Distr.: Near R. Zaire (Congo), Sumba, 0 m., 1925, *J. Gossweiler* 8985 (BM, sterile). Bié Distr.: Vila da Ponte (Fte. P. Amelia), R. Cuanze, 1905, *J. Gossweiler* 1948 (BM; Coi). Huila Distr.: Near Catumba, c. 1,150–1,700 m., 1860, *F. Welwitsch* 248 (BM; Coi, sterile; K, sterile). R. Cunene, Kilevi, 1885, *H. Schinz* 1001 (AM; K, sterile). R. Cunene, near Mutano (Humbe), 1,100 m., 1899, *H. Baum* 96 (BM; Coi; K).

SOUTH WEST AFRICA. Herero country: R. Okavango, Niangana, 1934, *K. Dinter* 7203 (K, sterile).

BECHUANALAND PROTECTORATE. Maun, R. Linyanti (Chobe), 1930, *G. Van Son* in *Herb. Transv. Mus.* 28986 (BM; NHP).

*P. octandrus* is essentially a palaeotropical species, with a wide distribution in Tropical and north-eastern South Africa\*, Madagascar, south-eastern Asia, and north-eastern Australia. It was originally described (as *Hydrogeton heterophyllus*) from Cochinchina.

This species has generally been known by the name *P. javanicus*, but unfortunately the earlier *P. octandrus* must take precedence despite the fact that the flowers have four stamens as in other Potamogetons. Loureiro, who first described the plant, was aware of its affinity with *Potamogeton*, but believing it had eight stamens he treated it as the type of a new genus under the name *Hydrogeton heterophyllus*. Poiret correctly reduced *Hydrogeton* to *Potamogeton* and renamed the species *P. octandrus*, as the combination *P. heterophyllus* was already in use for another species. His unhappy choice of epithet was due to

\* I have seen the following specimens from South Africa:—TRANSVAAL: *J. Burt Davy* 1613 (K; NHP 23); *C. E. Moss* 8535 (AM); *W. Nelson* 290 (K); *R. Schlechter* 4780 (AM; BM; Coi; K; NHP; Up). NATAL: *J. Medley Wood* 4300 (BM; K; NHP; SAM 23667); *R. Schlechter* 3125 (AM; BM; K; NHP); *F. Wilms* 2370 (BM; K).

his acceptance of Loureiro's erroneous statement about the number of anthers. Loureiro's type-specimen is preserved in the British Museum Herbarium and is identical with *P. javanicus* \*.

In Tropical Africa *P. octandrus* has a scattered distribution, extending from Nigeria, Oubangui-Chari, and the southern parts of the Anglo-Egyptian Sudan southwards to South West Africa, Bechuanaland Protectorate, and Southern Rhodesia. This distribution is of a different type from that of the other Tropical African Potamogetons, which are concentrated chiefly in the mountain and lake region of the east and in the Subtemperate regions of the north and south.

*P. octandrus* is one of the species with dimorphic leaves. Linear submersed leaves are always present and usually predominate. In mature (flowering and fruiting) plants coriaceous floating leaves are usually present also, but their degree of development varies. Sometimes they are numerous and conspicuous, sometimes few. In some examples the uppermost or 'involucral' leaves are only slightly dilated (as in *Barter* 1069, *Simpson* 7701, and *Taylor* 3326), while occasionally (as in *Preuss* 451) the dilation of these leaves is scarcely perceptible. Immature (sterile) plants commonly lack floating leaves altogether. Specimens in which floating leaves are absent or only poorly developed are easily distinguished from the true linear-leaved species *P. trichoides*, *P. hoggarensis*, and *P. panormitanus* by the presence of a well marked lacunar system running along both sides of the midrib of the leaves and usually extending sideways to the lateral nerves; a lacunar system sometimes borders the midrib in the three species mentioned, but it is narrow and does not extend to the lateral nerves except occasionally in the uppermost ('involucral') leaves of *P. panormitanus*.

Two gatherings of *P. octandrus* from the British Cameroons (*Preuss* 451, in flower, and *Staudt* 462, sterile), both lacking clearly developed floating leaves, were misunderstood by A. Bennett, who in the 'Flora of Tropical Africa' referred them to a new species, *P. Preussii*, under which he also included specimens of *P. panormitanus* from Eritrea and Abyssinia. Hagström (Crit. Res. 114-115) retained *P. Preussii* and suggested that Barter's plant from Nigeria (in Herb. Stockholm.) might be of a hybrid origin, but he had seen no fruit and obviously was unaware that the Kew specimen of *Barter* 1069 bears well developed fruits conforming with those of *P. octandrus*.

The name *P. huillensis* was given in manuscript by Welwitsch to his no. 248 from Angola; it was published by Schinz in 1891 as a synonym of *P. javanicus*. Another Angolan gathering (*Baum* 96, with well developed floating leaves) was referred by Bennett to his *P. javanicus* var. *major*.

3. POTAMOGETON TRICHOIDES Cham. & Schlecht. in *Linnaea*, ii, 175, t. 4 fig. 6 (1827). Hagstr. Crit. Res. 74, fig. 29 (1916). A. Peter in *Abhandl. Ges. Wiss. Götting., Math.-Phys. Kl., Neu. Folg.* xiii, 2, 108 (1928); in *Fedde, Repert. Sp. Nov., Beih.* xl, 1, 113 (1929).

\* See Merrill in *Trans. Amer. Phil. Soc., new ser.* xxiv, 2, 69 (1935).

KENYA. Kikuyu Prov.: Kiambu Distr., Ngong Forest, Karen Pond, c. 1,800 m., 1934, *G. Taylor* 1594a (BM) and 1595 (BM).

UGANDA. Western Prov.: Kigezi Distr., L. Bunyonyi, c. 2,000 m., 1933, *A. S. Thomas* 1216 (K).

SOUTHERN RHODESIA. Mashonaland: Lomagundi Distr., c. 1,050 m., 1921, *F. Eyles* 3141 in part \* (BM, sterile; SAM 26532 in part, sterile).

This species is widely distributed in western and central Europe, and is found also in Palestine, Kashmir, western North Africa, and eastern Tropical and South Africa as far south as Cape Province †. It was originally described from Europe ('a Rossia ad Galliam').

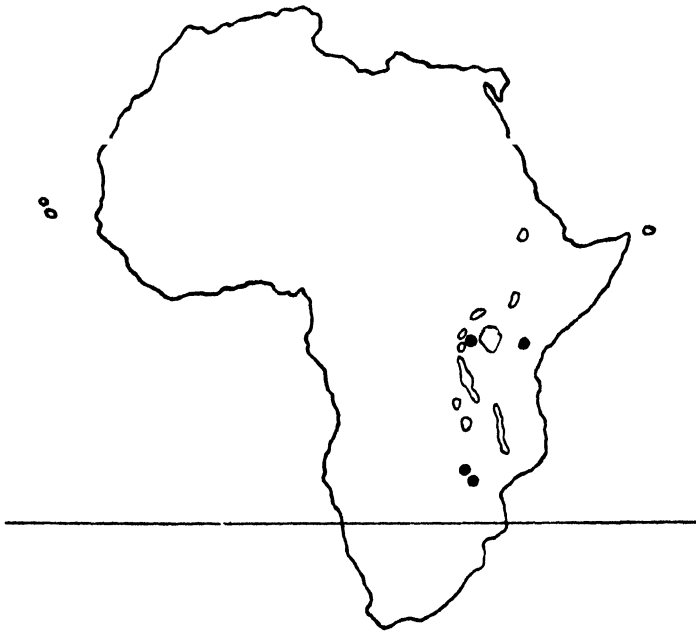


FIG. 3.—Distribution in Tropical Africa of *Potamogeton trichoides* Cham. & Schlecht.

*P. trichoides* was not included in the 'Flora of Tropical Africa'. The only Tropical African records to date are those published in 1928 and 1929 by A. Peter, whose material, stated to be in the fruiting condition, was collected by himself at the Cleveland Dam, in Salisbury District, Southern Rhodesia. I have not seen his plant (*A. Peter* 30692), but I have examined sterile material

\* This gathering comprises sterile material of both *P. trichoides* and *P. panormitanus*.

† I have seen *J. F. Drège* 8800 (K) and *F. H. Holland* 4169 (AM), both from the Uitenhage District of Cape Province. *Drège* 8800 was collected in the Zwartkops R. Hagström (Crit. Res. 77) correctly cited this *Drège* number under *P. trichoides*, but gave the locality as 'Port Natal'. I have also examined *C. E. Moss* 2519 (BM), from the Klip R., southern Transvaal; this is a mixture of *P. trichoides* and *P. panormitanus*.

collected by Eyles in the neighbouring District of Lomagundi. In addition, I have seen specimens from one station in Kenya and one in Uganda. Probably the species occurs in other localities where its presence has so far been overlooked. It is certainly a plant to be looked for in East Africa.

4. *POTAMOGETON HOGGARENSIS* Dandy, sp. nov.; *caule* ramoso, tereti vel subtereti, filiformi diametro infra 1 mm.; *foliis* submersis, sessilibus, anguste linearibus, apice acutis, margine integris, usque ad c. 110 mm. longis et 2.5 mm. latis, flaccidis, pellucidis, 3-5-nerviis, costa saepe lacunis elongatis pauciseriatis marginata, nervis lateralibus quam costa multo tenuioribus; *stipulis* a folio liberis, vaginam propriam formantibus, vagina aperta convoluta lineari apice

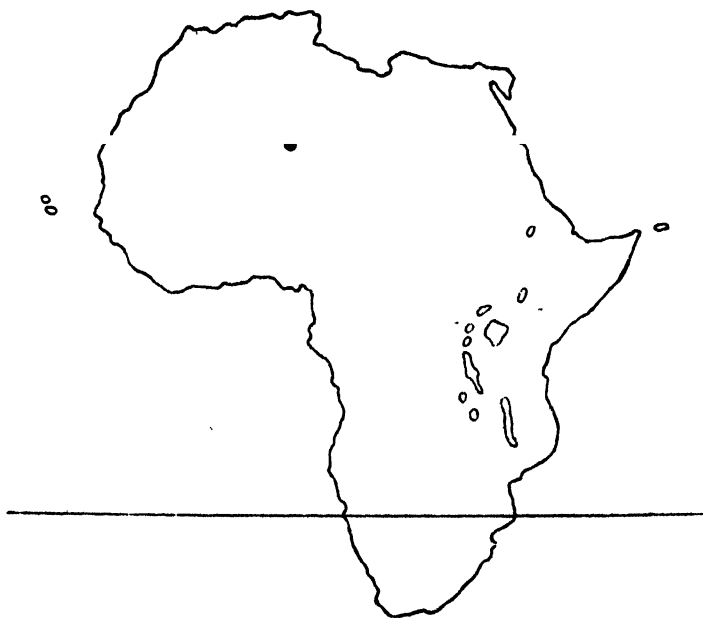


FIG. 4.—Distribution of *Potamogeton hoggarensis* Dandy.

rotundata multinervia (nervis in spatio intercarinali c. 7-11) demum long. c. 20-30 mm. attingenti diu persistenti in siceo brunnescenti; *floribus fructibusque* non adhuc notis.

*Potamogeton pusillus* (non L.).—Maire in Mém. Soc. Hist. Nat. Afr. Nord, iii, 53 (1933), pro parte.

ALGERIA. Territoires du Sud: Ahaggar, Imarera, 1,950-2,000 m., 1928, R. Maire 1226 (Alg, sterile, type; BM, sterile).

This interesting plant is known to me only from Maire's material, which unfortunately is sterile. It clearly represents a 'pusilloid' species—i.e. a species of the section *Chloephylli*—but certainly not *P. pusillus* L., to which Maire himself referred it. I am unable to match the plant with any other

known form, and therefore describe it as new. In the absence of flowers or fruits the exact position of the new species is doubtful, but the open and convolute stipular sheaths show that its affinities are not with *P. panormitanus* (which also occurs in Ahaggar) but with *P. trichoides*, *P. pusillus*, or *P. octandrus*. The stipular sheaths attain a length of about 2–3 cm. at maturity and are much larger than those of *P. pusillus* or *P. octandrus*. They are subsistent, as in *P. trichoides*, and much resemble the sheaths of that species except that the intercarinal area ('front-field' of Hagström) has more numerous nerves. In sterile material of *P. trichoides* the sheaths sometimes exceed 2 cm. in length, but they are generally smaller than in *P. hoggarensis*. The leaves of *P. hoggarensis* are much broader than those of *P. trichoides* and recall some of the broader-leaved forms of *P. pusillus*.

The locality Imarera where Maire collected *P. hoggarensis* is only just south of the Tropic of Cancer, and the species possibly extends north of the Tropic.

5. *POTAMOGETON PANORMITANUS* Biv. Nouv. Pi. 6 (1838) \*. Hagstr. Crit. Res. 98 (1916). Hutch. in Hutch. & Dalziel, Fl. W. Trop. Afr. ii, 307 (1936).

? *Potamogeton denticulatus* Link in Buch, Phys. Besch. Canar. Ins. 138, 173 (1825).

*Potamogeton gracilis* Fr. Novit. Fl. Suec., ed. 2, 50 (1828)—non *P. gracilis* Wolfg. (1827).

*Potamogeton pusillus* (non L.).—Hochst. in Flora, xxiv, Intelligenzbl. 1, 21 (1841). Webb in Hook. Niger Fl. 181 (1849). A. Rich. Tent. Fl. Abyssin. ii, 354 (1851). J. A. Schmidt, Beitr. Fl. Cap Verd. Ins. 167 (1852). Engl. in Phys. Abhandl. K. Akad. Wiss. Berl. 1891, 2, 110 (1892); Hochgebirgsfl. Trop. Afr. 110 (1892); in Engl. & Drude, Veg. Erd. IX, ii, 95 (1908). Schweinf. in Phys. Abhandl. K. Akad. Wiss. Berl. 1893, 2, 77 (1893); in Bull. Herb. Boiss. ii, App. 2, 7 (1894). Dur. & Schinz, Consp. Fl. Afr. v, 496 (1894), pro parte. A. Benn. in Dyer, Fl. Trop. Afr. viii, 222 (1901), pro parte. Gibbs in Journ. Linn. Soc., Bot. xxxvii, 474 (1906). Battand. & Trab. in Bull. Soc. Bot. Franc. liii, Sess. Extraord. 23 (1907). Graebn. in Engl. Pflanzenr. iv, 11, 113 (1907), pro parte. Rendle in Journ. Linn. Soc., Bot. xl, 221 (1911). Eyles in Trans. R. Soc. S. Afr. v, 293 (1916). Diels in Engl. Bot. Jahrb. liv, Beibl. 120, 63 (1917). A. Chev. Explor. Bot. Afr. Occ. Franç. i, 687 (1920). Norman in Journ. of Bot. lxii, 135 (1924). Broun & Massey, Fl. Sudan, 367 (1929). Maire in Bull. Mus. Nation. Hist. Nat., sér. 2, iii, 522 (1931); in Mém. Soc. Hist. Nat. Afr. Nord, iii, 53 (1933), pro parte.

*Potamogeton Preussii* A. Benn. loc. cit. (1901), pro parte, excl. pl. ex Cameroons. Graebn. tom. cit. 106 (1907), pro parte. Engl. in Engl. & Drude, loc. cit. (1908), pro parte.

*Potamogeton pusillus* var. *africanus* A. Benn. in Annu. Conserv. & Jard. Bot. Genève. ix, 102 in obs. (1905). Graebn. apud Mildbr. in Wiss. Ergebn. Deutsch. Z.-Afr. Exped. ii, 42 (1910).

\* This reference is taken from Hagstrom (Crit. Res. 98). I have not seen Bivona's description.

*Potamogeton panormitanus* f. *austrinus* Hagstr. op. cit. 102 (1916).

*Potamogeton antaicus* Hagstr. op. cit. 105, fig. 41 (1916).

*Potamogeton pusillus* var. *vulgaris* (non Fr.).—A. Chev. in Rev. Bot. Appliq. & Agric. Trop. xv, 1026 (1935).

CAPE VERDE ISLANDS. S. Antão : R. de João Afonso, 1864, R. T. Lowe (BM). R. Grande, 1864, Gray in Herb. R. T. Lowe (K). S. Thiago : 1873, H. N. Moseley (BM ; E ; K).

ALGERIA. Territoires du Sud : Ahaggar, Ft. Laperrine (Tamanrasset), 1933, J. Lauriol (Alg, sterile).

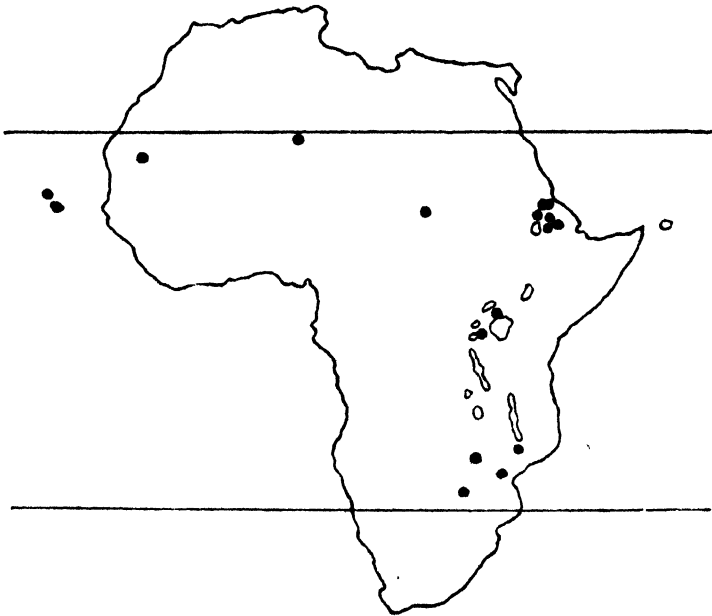


FIG. 5.—Distribution in Tropical Africa of *Potamogeton panormitanus* Biv

FRENCH WEST AFRICA. Mauritanie : Adrar, 1911–12, G. Schmitt in Herb. A. Chevalier 28594 (ex A. Chevalier under *P. pusillus*, and ex Hutchinson).

ANGLO-EGYPTIAN SUDAN. Darfur Prov. : Marra Mts., below Nyuringya, c. 1,700 m., 1921, H. Lynes 7 (BM ; K).

ERITREA. Saganeiti, Gorge de Degerra, 2,200 m., 1892, G. A. Schweinfurth & D. Riva 896 (K, syntype of *P. Preussii*).

ABYSSINIA. Near Aduwa, 1837, W. Schimper 179 (BM, syntype of *P. Preussii* ; K, syntype of *P. Preussii* ; Up, syntype of *P. panormitanus* f. *austrinus*). Shire, 1862, R. Quartin-Dillon & A. Petit 571 (K, syntype of *P. Preussii*). Sohi Farres (Mensach), c. 2,000 m., 1862, W. Schimper 530 (BM). Amba Sea, c. 1,850 m., 1856, W. Schimper 570 (K, syntype of *P. Preussii*).

UGANDA. Buganda Prov. : Entebbe Distr., L. Victoria, Entebbe, c. 1,150 m., 1930, J. D. Snowden 1836 (K, sterile).



BELGIAN CONGO. Ruanda Distr.: South-east of Karisimbi, L. Kalago, c. 2,300 m., 1907, *J. Mildbraed* 1545 (ex *Graebner* under *P. pusillus* var. *africanus*).

NYASALAND. Southern Prov.: Zomba Distr., Zomba, Residency gardens, 1895, *A. Whyte* (K).

PORTUGUESE EAST AFRICA. Companhia Moçambique: Gazaland, R. Inyamadzi, c. 750 m., 1906, *M. F. S. Swynnerton* 958 (BM, sterile).

SOUTHERN RHODESIA. Mashonaland: Lomagundi Distr., c. 1,050 m., 1921, *F. Eyles* 3141 in part \* (BM, sterile; NHP, sterile; SAM 26532 in part, sterile). Matabeleland: Matobo Distr., Matopo Hills, c. 1,350–1,500 m., 1905, *L. S. Gibbs* 190 (BM).

*P. panormitanus* has a wide geographical range in Europe, northern and eastern Africa (southwards to Cape Province †), Temperate and south-western Asia, and North America where it extends south as far as Mexico and Cuba. It was based on a plant from Palermo (*Panormus*), in Sicily.

By many authors this species has been confused with the exclusively North Temperate *P. pusillus* L., a circumstance which explains most of the numerous records of *P. pusillus* from Tropical Africa ‡. In 1916 Hagström (Crit. Res. 98–103) published an excellent account of *P. panormitanus* in which he pointed

\* This gathering comprises sterile material of both *P. panormitanus* and *P. trichoides*.

† South African specimens include *P. badius* Hagstr. Crit. Res. 104, fig. 40 (1916). I have seen the following:—TRANSVAAL: *M. C. Gillett* 3000 (NHP); *E. Marais* (NHP); *C. E. Moss* 9681 (AM; BM); *A. Rehmann* 4024 (BM; K); *R. Schlechter* 4405 (AM; BM; Coi; K; SAM 46415; Up) and 4695 (AM; BM; Coi; K; NHP; SAM 46373; Up); *F. Wilms* 1656 (BM; K) and 1657 (BM; K); without collector (NHP 25). NATAL: *J. F. Drege* 4458 (BM; K); *J. Medley Wood* 941 (K; SAM 23674) and 3055 (K) in *Herb. Natal Bot. Gard.* 479 (BM). ORANGE FREE STATE: *G. C. H. Barrett-Hamilton* (BM). BASUTOLAND: *A. Dieterlen* 1033 (BM, sterile; NHP, sterile; SAM 7172, sterile). CAPE PROVINCE: *R. Baur* 919 (K) and without no. (SAM 23675); *W. J. Burchell* 669 (K); *J. F. Drège* 1206 (BM; K; SAM 23676); *H. G. Flanagan* 2189 (NHP; SAM 23681), 2374 (AM; K; NHP), and 2492 (NHP; SAM 23679); *E. E. Galpin* 2283 (AM; NHP); *H. B. Gilliland* A123 (BM); *J. Leighton* (BM, sterile); *F. R. Long* 1145 (K); *P. MacOwan* 3167 in *Herb. Austro-Afr.* Cent. XX. 1992 (AM; BM; K; SAM 23673); *T. V. Paterson* 945 (AM) and 946 (AM); *H. H. W. Pearson* 1541 (SAM 1194); *A. Pegler* 2042 (NHP); *R. Schlechter* 6272 (AM; BM; K); *T. R. Sim* 1151 (SAM 23680); *W. Tyson* 1807 (AM).

‡ Not all the Tropical African records of *P. pusillus* refer to *P. panormitanus*. Exceptions are the records from Guinea (Cape Coast) published by Benthām (in Hook. Niger Fl. 528 (1849)), Durand and Schinz (Consp. Fl. Afr. v, 496 (1894)), and A. Bennet\* (in Dyer, Fl. Trop. Afr. viii, 222 (1901)), all of which were based on a specimen collected at Cape Coast, in the Gold Coast, by G. Don. This plant, which is preserved in the British Museum Herbarium, is referable to *Ruppia maritima* L. It was seen by Bennett, who included it under *P. pectinatus* in the 'Flora of Tropical Africa' (p. 223) though on the preceding page, under *P. pusillus*, he cited 'Guinea, ex Durand & Schinz', which refers to the same specimen!

In the above three works *P. pusillus* was also recorded from Angola, following Kunth, Enum. Pl. iii, 137 (1841). The origin of Kunth's record is obscure. I have seen no Angolan material of *P. panormitanus*, but *P. pectinatus* and *P. octandrus* (without floating leaves) might conceivably be mistaken for *P. pusillus*, and both occur in Angola.

Maire's records of *P. pusillus* from the central Sahara (in Mém. Soc. Hist. Nat. Afr. Nord, iii, 53 (1933)) include his no. 1226, from Ahaggar, which in the present paper is treated as the type of a new species, *P. hoggarensis* (see p. 522).

out its differences from *P. pusillus* and clearly established its claims to rank as a distinct species belonging to quite a different series. It may be noted here, however, that *P. panormitanus* is possibly conspecific with the earlier *P. denticulatus* Link, a species based on a Canary Islands plant whose identity is doubtful. A. Bennett, in Journ. of Bot. xxxiii, 138 (1895), expressed the opinion that Link's species should be referred to *P. trichoides*. *P. denticulatus* was published two years before *P. trichoides* and would replace that name if Bennett's view were found to be correct.

In north-western Tropical Africa *P. panormitanus* occurs in the Cape Verde Islands and in the mountains of the Sahara. On the eastern side it is found in the Marra Mountains of Darfur and in Eritrea and Abyssinia, whence it extends southwards through East Africa to Portuguese East Africa and Southern Rhodesia.

Six gatherings of the species were seen by Bennett in preparing his account of *Potamogeton* for the 'Flora of Tropical Africa'. Two of these, collected by Darwin in the Cape Verdes and Whyte in Nyasaland, were referred to *P. pusillus*. The other four (*Schweinfurth & Riva* 896 from Eritrea, *Schimper* 179 and 570 and *Quartin-Dillon & Petit* 571 from Abyssinia) were unaccountably treated as specifically distinct and included under the new species *P. Preussii* which was based on a form of *P. octandrus* from the (British) Cameroons.

*P. panormitanus* shows considerable variation in the breadth of the leaves. In Tropical Africa it tends to have comparatively broad leaves, in accordance with Hagström's statement (Crit. Res. 102) that the broad-leaved forms seem to spread southward from the Mediterranean and the narrow-leaved to the north of it. An Abyssinian plant collected by Schimper (no. 179) \* near Aduwa was referred by Hagström to a new African forma *austrius* characterized by the breadth of its leaves. In the same work he described a plant from the Cape Verde Islands, collected by Lowe in S. Antão, as a new species under the name *P. antaicus*. I am unable to distinguish this from *P. panormitanus*.

*Note.*—The stipules of *P. panormitanus* provide an infallible character by which this species may be distinguished from all other Tropical African *Potamogetons*. In the young state the stipules form a *closed tubular* sheath which embraces the stem immediately above the node. At a later stage the sheath may become ruptured, hence its structure should be investigated only in young shoots. In dried material the upper portion of a branch should be soaked and carefully dissected.

### Sect. III. HETEROPHYLLI Koch.

6. *POTAMOGETON SCHWEINFURTHII* A. Benn. in Dyer, Fl. Trop. Afr. viii, 220 (1901); apud Rendle in Journ. Linn. Soc., Bot. xxxviii, 23 (1907). Broun, Cat. Sudan Flow. Pl. 86 (1906). Graebn. in Engl. Pflanzenr. iv, 11, 79, fig. 19

\* This is one of the gatherings referred to *P. Preussii* by Bennett; see above,

(1907). Engl. in Engl. & Drude, Veg. Erd. IX, ii, 95 (1908). Broun & Massey, Fl. Sudan, 367 (1929). Hutch. in Hutch. & Dalziel, Fl. W. Trop. Afr. ii, 307 (1936).

*Potamogeton lucens* ? L.—Thoms. in Speke, Journ. Discov. Source Nile, 651 (1863).

*Potamogeton lucens* L. ?—Aschers. & Schweinf. in Schweinf. Beitr. Fl. Aethiop. i, 292 (1867).

*Potamogeton lucens* (non L.).—Bak. in Trans. Linn. Soc. Lond. xxix, 158 (1875). Dur. & Schinz, Consp. Fl. Afr. v, 494 (1894). Schweinf. in Bull. Herb. Boiss. ii, App. 2, 7 (1894). A. Benn. in Journ. of Bot. xxxiii, 138 (1895); in Dyer, tom. cit. 221 (1901). K. Schum. in Engl. Pflanzenw. Ost-Afr. C, 93 (err. *lucers*) (1895). C. H. Wright in Johnston, Uganda Protect. i, 348 (1902). Graebn. tom. cit. 76 (1907), pro parte; apud Mildbr. in Wiss. Ergebn. Deutsch. Z.-Afr. Exped. ii, 42 (1910). Engl. in Engl. & Drude, loc. cit. (1908). Dinter in Fedde, Repert. Sp. Nov. xxii, 383 (1926). A. Peter in Abhandl. Ges. Wiss. Götting., Math.-Phys. Kl., Neu. Folg. xiii, 2, 108 (1928); in Fedde, op. cit., Beih. xl, 1, 113 (1929). Broun & Massey, loc. cit. (1929). Robyns in Ann. Soc. Sci. Brux., sér. B, lv, 305 (1935). Dandy apud Jenkin in Ann. & Mag. Nat. Hist., ser. 10, xviii, 177 (1936).

*Potamogeton capensis* Scheele ex [A. Benn. in Ann. K. K. Naturhist. Hofmus. Wien, vii, 287 (1892), *nomen nudum*] Hagstr. Crit. Res. 203, fig. 101 (1916).

*Potamogeton lucens* var. *fluitans* (non Coss. & Germ.).—A. Benn. in Dyer, Fl. Cap. vii, 48 (1897); in Dyer, Fl. Trop. Afr. viii, 221 (1901).

*Potamogeton lucens* subvar. *longifolius* (Gay) Graebn. in Engl. Pflanzenr. iv, 11, 78 (1907), pro parte.

*Potamogeton repens* Hagstr. apud R. E. Fr. in Wiss. Ergebn. Schwed. Rhodes.-Kongo-Exped. i, 185, fig. 15 (1916); Crit. Res. 170, figs. 87–88 (1916).

*Potamogeton nodosus* f. *angustissimus* Hagstr. apud R. E. Fr. tom. cit. 186 (1916); Crit. Res. 188 (1916).

FRENCH WEST AFRICA. Senegal: L. Guier, 1819, *Roger* (BM; K); 1826, *F. R. Leprieur* (BM; K).

ANGLO-EGYPTIAN SUDAN. Upper Nile Prov.: L. No. near the Suddite Factory, 1929, *N. D. Simpson* 7204a (BM\*; K\*). Bahr el Ghazal, near Nuer villages, 1869, *G. A. Schweinfurth* 1165 (K\*, syntype). Bahr el Arab, Ghabat el Arab, 1929, *N. D. Simpson* 7204b (BM\*); 1930, *N. D. Simpson* 7665 (BM\*; K\*). Equatorial Prov.: Bahr el Ghazal, mouth of Bahr el Arab, 1869, *G. A. Schweinfurth* 1223 (BM\*, photo; E, sterile; K\*, lectotype).

ERITREA. Asmara, 2,300 m., 1892, *G. A. Schweinfurth* & *D. Riva* 2110 (K, sterile).

ABYSSINIA. L. Tana, near Angasha, 1863, *W. Schimper* 1359 (BM\*, syntype; E\*; K\*, syntype).

KENYA. Nyanza Prov. : L. Victoria, 1928, *M. Graham* H.47-28 in part ‡ (K). Naivasha Prov. : L. Naivasha, c. 1,850 m., 1930, *E. R. Napier* 470 (K). L. Naivasha, 1929, *P. M. Jenkin* (BM) ; 1931, *R. E. Dent* (BM). Kikuyu Prov. : Kiambu Distr., Ngong Forest, Karen Pond, c. 1,800 m., 1934, *G. Taylor* 1594 (BM). Ukamba Prov. : Machakos Distr., Kibwezi, c. 900 m., 1921, *R. A. Dummer* 4577 (K).

UGANDA. Eastern Prov. : Lango Distr., Victoria Nile, Atura, 1930, *L. C. C. Liebenberg* 225 (K). Northern Prov. : Bunyoro Distr., junction of Victoria Nile and L. Albert, 1935, *G. Taylor* 3358a (BM \*). Bunyoro Distr., Victoria Nile, Mutunda, 1935, *W. J. Eggeling* E.2233 (BM \*). Bunyoro Distr., sides



FIG. 6.—Distribution in Tropical Africa of *Potamogeton Schweinfurthii* A. Benn.

of Victoria Nile. 2° N., 1862, *J. H. Speke & J. A. Grant* (K, sterile). Buganda Prov. : Mengo Distr., Luzila, 1929, *L. C. C. Liebenberg* 750 (K †). Entebbe Distr., Entebbe, c. 1,200 m., 1905, *E. Brown* 223 (K). Entebbe Distr., Sese Is., Bugala I., 1922, *T. D. Maitland* 367 (K, sterile). Entebbe Distr., Sese Is., Fumve I., c. 1,150 m., 1934, *A. S. Thomas* 1226 (K). Western Prov. : Kigezi Distr., L. Bunyonyi, c. 2,000 m., 1933, *A. S. Thomas* 1211 (K, sterile). Kigezi Distr., L. Bunyonyi, c. 1,950 m., 1929, *J. D. Snowden* 1507 in part § (BM ; K,

\* With coriaceous floating leaves.

† With intermediate 'semi-floating' leaves.

‡ This gathering also includes material of *Vallisneria*.

§ This gathering consists mainly of *P. nodosus*,

sterile). Kigezi Distr., L. Bunyonyi, 1931, *E. B. Worthington* (BM). Kigezi Distr., L. Bunyonyi, Bufundi, 1927, *D. H. Linder* 2590 (K).

BELGIAN CONGO. Katanga Prov. : Tanganika Moero Distr., L. Tanganyika, Albertville, 1927, *D. H. Linder* 1922 (K).

TANGANYIKA TERRITORY. Lake Prov. : Bukoba Distr., L. Victoria, Bukoba, 1905, *W. A. Cunningham* 56 (BM, sterile). Western Prov. : Kigoma Distr., L. Tanganyika, mouth of R. Malagarasi, 1905, *W. A. Cunningham* 45 (BM). Central Prov. : Manyoni Distr., Kazikazi, c. 1,200 m., 1931, *B. D. Burtt* 3345 (K). Lindi Prov. : Songea Distr., L. Nyasa, Lukoma, 1887, *W. Bellingham* (BM †).

NYASALAND. Northern Prov. : Kota Kota Distr., L. Nyasa, off Kota Kota, 1904, *W. A. Cunningham* 8 (BM \*). Northern Prov. or Southern Prov. : West shore of L. Nyasa, south-western bay, 1861, *J. Kirk* (K †). Southern Prov. : South Nyasa Distr., L. Nyasa, south-east arm near anchorage, 1904, *W. A. Cunningham* 2 (BM †).

NORTHERN RHODESIA. Mweru Luapula Prov. : L. Bangweulu, near Kasomo, 1911, *R. E. Fries* 655 (BM, photo ; Up, sterile, type of *P. repens*). Batoka Prov. : Kazungula, R. Zambesi, 1927. *M. E. Blenkinson* in *Herb. C. E. Moss* 16406 (BM \*).

SOUTHERN RHODESIA. Mashonaland : Lomagundi Distr., Sinoia Cave, c. 1,200 m., 1921, *F. Eyles* 3161 (K, sterile). Matabeleland : Wankie Distr., R. Zambesi, above Victoria Falls, 1911, *R. E. Fries* 137 (BM \*, photo ; Up \*, sterile, type of *P. nodosus* f. *angustissimus*).

SOUTH WEST AFRICA. Herero country : R. Okavango, Niangana, 1934, *K. Dinter* 7241 (K). Otavi, 1924, *K. Dinter* 5254 (NHP).

*P. Schweinfurthii* is a species of wide distribution in Africa. On the eastern side of the continent it extends from Lower Egypt to Cape Province as far south as Uitenhage District ‡, and has been collected in numerous Tropical localities from Eritrea, Abyssinia, and the Anglo-Egyptian Sudan southwards to Southern Rhodesia. In the west it occurs in north-western Africa from Tunisia to Senegal, and also in Tropical South West Africa. Specimens from

\* With coriaceous floating leaves.

† With intermediate 'semi-floating' leaves.

‡ *P. capensis* Scheele ex Hagstr., cited in the synonymy given above, was based on a plant from the Zwartkops R., Uitenhage District. South African specimens also include *P. promontoricus* Hagstr. Crit. Res. 182, fig. 94 (1916) and *P. venosus* A. Benn. in Trans. & Proc. Bot. Soc. Edin. xxix, 52 (1924). I have seen the following :—PORTUGUESE EAST AFRICA (Lourenço Marques Distr.) : *H. Bolus* in *Herb. Norm. Austro-Afr.* 1393 (BM ; K ; SAM 23668 ; Up). TRANSVAAL : *W. Nelson* 224 (K) ; *F. Wilms* 1653 (K, sterile). NATAL : *J. Medley Wood* 1889 (K) and 3015 (K) in *Herb. Natal Bot. Gard.* 490 (BM) ; *H. Rudatis* 1381 (BM ; K) ; *R. Schlechter* 3120 (AM, sterile ; BM, sterile ; K, sterile). CAPE PROVINCE : *C. F. Ecklon & C. L. P. Zeyher* 640 (AM † ; BM \* ; K † ; SAM 23669 \*) ; *F. H. Holland* 611 (AM \*) ; *M. Wilman* in *McGregor Mus. Kimberley* 1252 (K ; NHP) ; *C. L. P. Zeyher* 4327 (SAM 4521). The specimens marked \* have coriaceous floating leaves ; those marked † have intermediate 'semi-floating' leaves ; the remainder lack floating or 'semi-floating' leaves.

Lake Guier, in north-western Senegal, were obtained by French botanists more than a century ago, and apparently these were the first examples of *P. Schweinfurthii* to be collected in Tropical Africa. Possibly the species occurs also in Madagascar, but the available material (a sterile specimen in the British Museum Herbarium, collected by J. V. Thompson) is too poor for a definite decision to be made.

The natural affinity of *P. Schweinfurthii* is with the North Temperate *P. lucens* L. and its allies, a relationship which is reflected in the fact that most of the African specimens have hitherto been referred to *P. lucens*. Unlike that species, however, *P. Schweinfurthii* is heterophyllous, for it can develop floating leaves although they are present in only a minority of the gatherings examined. In most specimens all the leaves are flaccid, pellucid, and submersed as in *P. lucens*, but in some individuals the upper leaves have coriaceous floating laminas, while in others the upper leaves are intermediate ('semi-floating') in character with more or less subcoriaceous laminas\*. The submersed leaves are narrower in shape than is normal in *P. lucens*, and vary remarkably in the degree of development of the petiole. They may be sessile, short-petioled, or long-petioled, and considerable variation is often seen in a single plant. The floating and 'semi-floating' leaves always have a more or less elongated petiole. (See Pls. 21 & 22.)

*P. Schweinfurthii* was originally described by A. Bennett in the 'Flora of Tropical Africa' from three gatherings (*Schimper* 1359 from Abyssinia, and *Schweinfurth* 1223 † and 1165 from the Sudan) all of which were characterized by the presence of coriaceous floating leaves. In the same work he also dealt with six other gatherings of the species, but these lacked coriaceous floating leaves and he therefore placed them under *P. lucens*, *Schweinfurth* & Riva's no. 2110 from Eritrea and Speke & Grant's plant from the Victoria Nile being referred to *P. lucens* proper whilst the specimens collected by Roger and Leprieur in Senegal and by Bellingham and Kirk in Lake Nyasa were identified with *P. lucens* var. *fluitans* Coss. & Germ. (*P. longifolius* Gay ex Poir.). The latter is a narrow-leaved European form of *P. lucens* which superficially bears so close a resemblance to *P. Schweinfurthii* that Gay himself determined the Senegal plants as *P. longifolius*.

The name *P. capensis* was given in manuscript by Scheele to a plant of *P. Schweinfurthii* from Cape Province, and was first published by Bennett in 1892 as a *nomen nudum*. In 1916 Hagström, who apparently had not seen authentic material of *P. Schweinfurthii*, described and figured *P. capensis* from South African specimens, citing *P. Schweinfurthii* as a doubtful synonym. Hagström had, however, already dealt with two sterile gatherings of

\* As an indication to the reader, specimens with floating or 'semi-floating' leaves are distinguished respectively by the signs \* and † in the lists of both Tropical and South African material given above.

† A specimen (Sheet 1) of this number in Herb. Kew. is here chosen as lectotype of *P. Schweinfurthii*.

*P. Schweinfurthii* from Rhodesia without recognizing their true affinity. These were both collected by R. E. Fries (nos. 137 and 655). Hagström referred no. 137, which has dimorphic leaves, to *P. nodosus* as a new forma *angustissimus*. On the other hand, he treated no. 655 as a new species (*P. repens*) of the subsection *Sclerocarp*. This latter plant apparently represents a juvenile state; it has a creeping rhizome, and the leaves are all submersed and so small and narrow that only an examination of their venation reveals the identity of the plant with *P. Schweinfurthii*. A similar state of the species was collected by Eyles (no. 3161) in Sinoia Cave, Lomagundi District, Southern Rhodesia.

7. *POTAMOGETON NODOSUS* Poir. in Encycl. Méth., Bot., Suppl. iv, 535 (1816). Hagstr. Crit. Res. 183, fig. 95 (1916), pro parte.

*Potamogeton natans* L. Sp. Pl. i, 126 (1753), pro parte, quoad var.  $\beta$ . Hochst. in Flora, xxiv, Intelligenzbl. 1, 21 (1841). A. Rich. Tent. Fl. Abyssin. ii, 354 (1851). A. Benn. in Journ. of Bot. xxxiii, 138 (1895); apud Gibbs in Journ. Linn. Soc., Bot. xxxvii, 474 (1906). Graebn. in Engl. Pflanzenr. iv, 11, 42 (1907), pro parte; apud Mildbr. in Wiss. Ergebn. Deutsch. Z.-Afr. Exped. ii, 41 (1910). Eyles in Trans. R. Soc. S. Afr. v, 293 (1916). A. Peter in Abhandl. Ges. Wiss. Götting., Math.-Phys. Kl., Neu. Folg. xiii, 2, 108 (1928); in Fedde, Repert. Sp. Nov., Beih. xl, 1, 113 (1929). Maire, Contrib. Étud. Fl. Tibesti, 6 (1935); in Mém. Acad. Sci. Inst. Franc., sér. 2, lxii, 6 (1936).

*Potamogeton fluitans* Roth, Tent. Fl. German. i, 72 (1788), pro parte, quoad pl. ex Hunte fluvio. A. Benn. apud Balf. f. in Trans. R. Soc. Edin. xxxi, 300 (1888); in Journ. of Bot. xxxiii, 138 (1895); in Dyer, Fl. Trop. Afr. viii, 219 (1901). K. Schum. in Engl. Pflanzenw. Ost-Afr. C, 93 (1895). Rendle in Cat. Afr. Pl. Welw. ii, 94 (1899). Engl. in Engl. & Drude, Veg. Erd. IX, ii, 95 (1908). Eyles, tom. cit. 292 (1916). A. Peter in Abhandl. Ges. Wiss. Götting., Math.-Phys. Kl., Neu. Folg. xiii, 2, 107 (1928); in Fedde, tom. cit. 112 (1929). Snowden in Journ. Ecol. xxi, 19 in obs. (1933).

*Potamogeton indicus* Roxb. [Hort. Bengal. 12 (1814), *nomen nudum*] Fl. Ind., ed. Carey, i, 471 (1820)—non *P. indicus* Roth ex Roem. & Schult. (1818).

*Potamogeton natans* var. *fluitans* Cham. Adnot. 4 (1815)\*. Dur. & Schinz, Consp. Fl. Afr. v, 495 (1894).

*Potamogeton americanus* Cham. & Schlecht. in Linnaea, ii, 226, t. 6 fig. 26 (1827). A. Benn. in Journ. of Bot. xxxi, 297 (1893), pro parte.

*Potamogeton Richardi* Solms in Schweinf. Beitr. Fl. Aethiop. i, 194 in obs. (1867). Aschers. & Schweinf. in Schweinf. tom. cit. 292 (1867). Engl. in Phys. Abhandl. K. Akad. Wiss. Berl. 1891, 2, 110 (1892); Hochgebirgsfl. Trop. Afr. 110 (1892); in Engl. & Drude, loc. cit. (1908). Dur. & Schinz, tom. cit. 496 (1894). A. Benn. op. cit. xxxiii, 139 in obs. (1895); in Dyer, loc. cit. (1901). Graebn. in Engl. Pflanzenr. iv, 11, 56 (1907). Hagstr. op. cit. 195 (1916). R. E. Fr. apud R. E. & T. C. E. Fr. in Notizbl. Bot. Gart. & Mus. Berl.-Dahl. viii, 662 (1924). Eggeling in Journ. Ecol. xxiii, 428 in obs. (1935).

\* This reference is copied from Durand and Schinz. I have not seen Chamisso's work.

*Potamogeton natans* subsp. *plantagineus* (Du-Croz) A. Benn. apud Balf. f. tom. cit. 299 (1888), pro parte.

*Potamogeton plantagineus* (non Du-Croz).—Engl. in Phys. Abhandl. K. Akad. Wiss. Berl. 1894, 1, 41 (1894); Glied. Veg. Usambara, 41 (1894); Pflanzenw. Ost-Afr. A, 80 in obs. (1895). Dur. & Schinz, tom. cit. 495 (1894), pro parte.

*Potamogeton americanus* var. *Richardi* (Solms) Solms ex Schweinf. in Bull. Herb. Boiss. ii, App. 2, 8 (1894).

*Potamogeton polygonifolius* (non Pourr.).—A. Benn. in Journ. of Bot. xxxiii, 138 (1895), pro parte. Graebn. tom. cit. 65 (1907), pro parte.

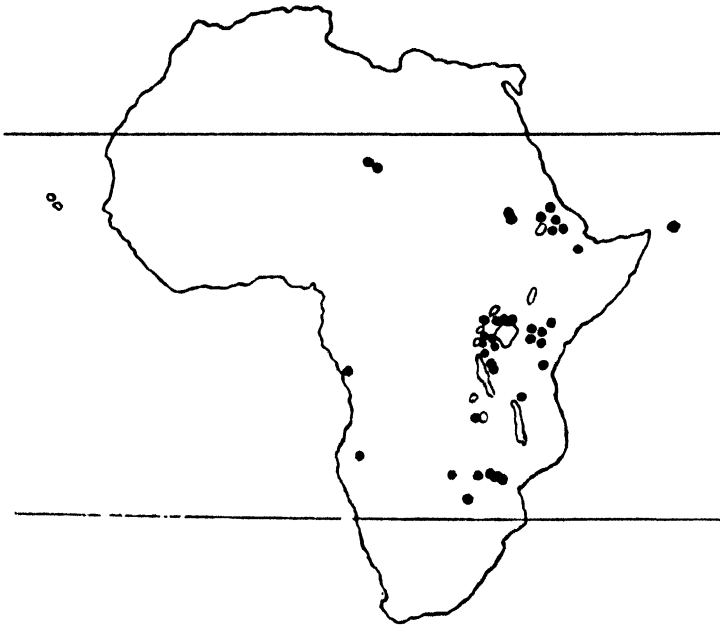


FIG. 7.—Distribution in Tropical Africa of *Potamogeton nodosus* Poir.

*Potamogeton coloratus* (non Hornem.).—A. Benn. in Dyer, tom. cit. 222 (1901). Graebn. tom. cit. 69 (1907), pro parte. A. Peter in Abhandl. Ges. Wiss. Götting., Math.-Phys. Kl., Neu. Folg. xiii, 2, 107 (1928); in Fedde, tom. cit. 113 (1929).

*Potamogeton fluitans* subsp. *americanus* (Cham. & Schlecht.) Graebn. tom. cit. 60 (1907), pro parte.

*Potamogeton semicoloratus* A. Benn. in Journ. of Bot. xlviii, 150 (1910). Hagstr. op. cit. 181 (1916).

*Potamogeton stagnorum* Hagstr. apud R. E. Fr. in Wiss. Ergebn. Schwed. Rhodes.-Kongo-Exped. i, 187, fig. 16 (1916); Crit. Res. 159, fig. 78 (1916).

FRENCH EQUATORIAL AFRICA. Tchad: Tibesti, Aozou, 880 m., 1931, *M. Dalloni* (Alg, sterile). Tibesti, Yebbi Bou, 1,300 m., 1931, *M. Dalloni* (Alg).



SOCOTRA. 1880, *I. B. Balfour* 2 (E, sterile), 3 (E), 168 (E), and without no. (BM).

ANGLO-EGYPTIAN SUDAN. Blue Nile Prov.: Gezira canals, 1936, *F. W. Andrews* A138 (K). Gezira, Abu Sin canal, 1936, *F. W. Andrews* A142 (K).

ERITREA. Saganeiti, Gorge de Degerra, 2,200 m., 1892, *G. A. Schweinfurth* & *D. Riva* 891 (K).

ABYSSINIA. Near Aduwa, 1837, *W. Schimper* 135 (type-collection of *P. Richardi*; BM; K). Amba Sea, c. 1,850 m., 1856, *W. Schimper* 571 (K). Addi Abun, c. 1,850 m., 1863, *W. Schimper* 958 (BM). Haramaia, 9° 24' N., 42° E., c. 2,000 m., 1933, *J. B. Gillett* 5471 (BM; K).

KENYA. Naivasha Prov. or Kikuyu Prov.: Aberdare Mts., c. 3,300 m., 1922, *R. E. & T. C. E. Fries* 2611 (Up). Kikuyu Prov.: Laikipia plateau and Aberdare range, district around Nyeri, 1908, *W. Scoresby Routledge* (K). Meru Distr., near Meru, 1922, *R. E. & T. C. E. Fries* 1800 (K; Up). Kiambu Distr., Limuru, c. 2,150 m., 1915, *R. A. Dummer* 1633 (BM; K); 1918, *J. D. Snowden* 607 (BM; K). Kiambu Distr., R. Ruira, c. 1,850 m., 1934, *G. Taylor* 1022 (BM).

UGANDA. Buganda Prov.: Mengo Distr., Kyadondo, near Magigze, c. 1,200 m., 1915, *R. A. Dummer* 2473 (BM; K). Mengo Distr., Kampala, King's Lake, c. 1,200 m., 1936, *G. L. Hancock & P. C. Chandler* 135 (BM; K). Mengo Distr., Kiagwe, Namanve, c. 1,150 m., 1932, *W. J. Eggeling* 503 (K). Mubende Distr., north of Kakumiro, c. 1,050 m., 1906, *A. G. Bagshawe* 954 (BM). Entebbe Distr., Entebbe, c. 1,200 m., 1905, *E. Brown* 333 (K). Western Prov.: Toro Distr., Fort Portal, 1932, *C. Hazel* 226 (K). Kigezi Distr., north-west end of L. Bunyonyi, 1934, *G. Taylor* 2174 (BM). Kigezi Distr., L. Bunyonyi, c. 1,950 m., 1929, *J. D. Snowden* 1507 in part \* (BM; K). Kigezi Distr., L. Bunyonyi, Bufundi, 1927, *D. H. Linder* 2594 (K).

BELGIAN CONGO. Congo-Kasai Prov.: Bas Congo Distr., Zaire (Congo), Vista, 1886, *M. Chaves* (Coi).

TANGANYIKA TERRITORY. Lake Prov.: Bukoba Distr., Kalema, c. 1,200 m., 1931, *A. E. Haarer* 2110 (K). Bukoba Distr., Kishanda, c. 1,350 m., 1931, *A. E. Haarer* 2337 (K). Iringa Prov.: Njombe Distr., Ukinga, Bulongwa, 2,000 m., 1914, *A. Stolz* 2462 (BM; K; NHP; Up).

NORTHERN RHODESIA. Mweru Luapula Prov.: R. Chimona, near its junction with L. Bangweulu, 1911, *R. E. Fries* 691 (BM, photo; Up, sterile, type of *P. stagnorum*).

SOUTHERN RHODESIA. Mashonaland: Salisbury Distr., Salisbury, 1898, *R. F. Rand* 540 (BM). Salisbury Distr., Cleveland Dani, c. 1,500 m., 1917, *F. Eyles* 659 (BM; K). Salisbury Distr., west of Salisbury, R. Macabusi, 1931, *H. B. Gilliland* 63 (BM). Umtali Distr., Manicaland, Penhalonga, Charity, c. 1,700 m., 1934, *H. B. Gilliland* 527.B (BM). Umtali Distr., Manica district, R. Odzani valley, *A. J. Teague* 571 (K). Matabeleland: Wankie Distr.,

\* This gathering includes fragments of *P. Schweinfurthii*.

R. Zambesi, Victoria Falls, c. 900 m., 1905, *L. S. Gibbs* 146 (BM). Matobo Distr., Matopo Hills, c. 1,500 m., 1904, *F. Eyles* 36 (BM). Matobo Distr., Matopo Hills, c. 1,350 m., 1912, *F. A. Rogers* 5677 (BM; K; SAM 8928). Matobo Distr., Matopo Hills, 1905, *L. S. Gibbs* 94 (BM, sterile).

ANGOLA. Huila Distr.: Mumpula, c. 1,150–1,700 m., 1859, *F. Welwitsch* 249 (BM, sterile; K, sterile).

This species is widely dispersed in the warmer parts of both Hemispheres, being found in central and southern Europe, Africa (from the Mediterranean to Cape Province\*), southern Asia, North and South America, and islands in the Pacific. It was based on material from the Canary Islands.

Numerous Tropical African gatherings of *P. nodosus* indicate a general distribution from Eritrea, Abyssinia, and the Anglo-Egyptian Sudan southwards through the mountain and lake region of East Africa to Southern Rhodesia. From Rhodesia the species extends westwards into southern Angola†, and there is a gathering (dated 1886) from the mouth of the Congo. Like *P. pectinatus* it occurs in the island of Socotra, and in recent years material has been collected in the massif of Tibesti in the eastern Sahara.

*P. nodosus*, as found in Tropical Africa, presents a fairly uniform appearance, yet in common with other large-leaved aquatic plants it displays a considerable amount of variation in the shape and size of the leaves, and this no doubt largely accounts for the variety of names which have been given to Tropical African specimens, some of which have been identified with such North Temperate species as *P. natans* L., *P. polygonifolius* Pourr., and *P. coloratus* Hornem. Mature (flowering and fruiting) plants of *P. nodosus* have mostly floating leaves, whose laminae range in shape from lanceolate to elliptic or oblong or ovate-oblong, with a base varying from cuneate to rounded or subcordate in which case the leaf approaches the form characteristic of *P. natans*. The lower leaves are submersed, but usually these soon disappear by decay or are torn away by motion of the water, though the petioles may remain. I have seen a sterile specimen from Socotra (*Balfour* 2 in Herb. Edinburgh.) in which all the leaves are thin in texture and pellucid, although the upper ones have the shape and size

\* South African specimens include *P. Thunbergii* Cham. & Schlecht. in *Linnaea*, ii, 221, t. 6 fig. 21 (1827)=*P. natans* var. *capensis* Dur. & Schinz, *Consp. Fl. Afr.* v, 494 (1894)=*P. americanus* var. *Thunbergii* (Cham. & Schlecht.) A. Benn. in *Dyer, Fl. Cap.* vii, 46 (1897), pro parte=*P. fluitans* proles *Thunbergii* (Cham. & Schlecht.) Graebn. in *Engl. Pflanzenr.* iv, 11, 61 (1907). I have examined the following:—TRANSVAAL: *R. D. Bradfield* 175 (NHP, sterile); *C. E. Moss* 12007 (BM, sterile); *W. Nelson* 514 (K); *A. Rehmann* 6578 (K) and 6801 (BM; K); *F. Wilms* 1652 (BM; K). NATAL: *J. Medley Wood* 3020 (K) in *Herb. Natal Bot. Gard.* 491 (BM); *F. Wilms* 2371 (BM; K). BASUTOLAND: *A. Dieterlen* 831 (BM; K; NHP; SAM 2744). CAPE PROVINCE: *L. Britten* 5033 (AM); *J. F. Drège* (BM; K); *H. G. Fourcade* 3312 (K); *F. R. Long* 503 (K; NHP 15142); *A. Rehmann* 2415 (BM; K).

† Probably it occurs in northern Bechuanaland Protectorate, but I have not seen specimens. Two gatherings from Maun, on the R. Linyanti (Chobe), were listed as '*Potamogeton nodosus* Poir.?' by Bremekamp and Obermeyer in *Ann. Transv. Mus.* xvi, 401 (1935); these were collected by G. Van Son (*Herb. Transv. Mus.* 28987 and 28988) in 1930.

of normal coriaceous floating leaves. No doubt this plant grew under unusual conditions, perhaps in extra-deep water.

The first herbarium material of *P. nodosus* to be collected in Tropical Africa was Schimper's no. 135 from Abyssinia, which was gathered in 1837 and four years later was referred to *P. natans* by Hochstetter in a published list of Schimper's plants. This identification cannot be regarded as entirely erroneous, for *P. nodosus* is Linnaeus's *P. natans* in part\*. Other Tropical African specimens have since been placed in *P. natans* by A. Bennett, Graebner, and A. Peter. In 1867 Solms proposed that Schimper's plant should be separated as a distinct species under the name *P. Richardi*. Schweinfurth in 1894 reduced *P. Richardi* to varietal status under *P. americanus* (*P. nodosus*), but most authors have accepted it as a valid species. Graebner, in 'Das Pflanzenreich' (p. 57), stated that *P. Richardi* differed from *P. fluitans* (including *P. nodosus*) in the larger leaves and larger more compressed fruits. These distinctions, however, certainly do not hold for the extensive series of specimens now available from Tropical Africa. The variation in leaf-size has already been mentioned; as for the fruiting-carpels, they vary from about 3 to 5.5 mm. in length as compared with a range of about 2.5 to 4.5 mm. in specimens of *P. nodosus* from outside Africa. It may be observed that in dried material the fruiting-carpels are generally more or less prominently three-keeled, but sometimes the keels are obscure, and it is probable that their degree of prominence is affected by the drying process. Hagström (Crit. Res. 195-196) retained *P. Richardi* as a distinct species of the *P. natans* group and considered that the anatomical diagram distinguished it from *P. nodosus*; but he had seen only two specimens.

Some of the Tropical African examples of *P. nodosus* have been referred to *P. fluitans*, and with justification, for *P. nodosus* is apparently *P. fluitans* Roth in part just as it is *P. natans* L. in part. Under *P. fluitans* Roth included the locality 'Hunte fluviu Ducatus Oldenburgensis' (in Germany) which is a station for *P. nodosus*, but according to Hagström (op. cit. 184) Roth's description does not fit specimens of *P. nodosus* but agrees rather with the hybrid *P. lucens* × *P. natans*. In this controversial matter I follow Hagström and accept *P. nodosus* as the valid name for the species under consideration.

The Tropical African records of *P. polygonifolius* and *P. coloratus* (including *P. plantagineus* Du-Croz ex Roem. & Schult.) are certainly erroneous and can only pertain to *P. nodosus*. *P. polygonifolius* and *P. coloratus* are North Temperate species which in Africa appear to be restricted to the north-western Temperate region (Algeria, Morocco, and the islands to the west). A form of *P. nodosus* collected by Balfour in Socotra was originally referred by Bennett, in 1888, to *P. natans* subsp. *plantagineus* (i.e. *P. coloratus*), but in 1910 he treated it, in conjunction with Arabian specimens of *P. nodosus*, as a new

\* Under *P. natans* Linnaeus (Sp. Pl. i, 126 (1753)) cited 'β. Potamogeton foliis lanceolato-oblongis, petiolis longis. Gron. virg. 139'. The reference is to Gronovius's 'Flora Virginea', p. 139 (1743), where J. Clayton's no. 664, from Virginia, is cited. Clayton's plant, which is preserved in the British Museum Herbarium, is a sterile specimen of *P. nodosus*.

species under the name *P. semicoloratus*. This was retained by Hagström (op. cit. 181), who provisionally considered it, in the absence of ripe fruits and young pistils, to be 'a connective link between the *Colorati* and the *Amplifolii*'.

*P. stagnorum* was based by Hagström on a sterile specimen of *P. nodosus* collected by R. E. Fries (no. 691) in Northern Rhodesia. Another sterile specimen, also gathered by Fries (no. 137) in Rhodesia, was treated by Hagström as a new forma *angustissimus* of *P. nodosus*, but this is referable to *P. Schweinfurthii*.

Bennett in Journ. of Bot. xxxiii, 138 (1895) reported *P. fluitans* from 'Lagos'. I do not know the origin of this record.

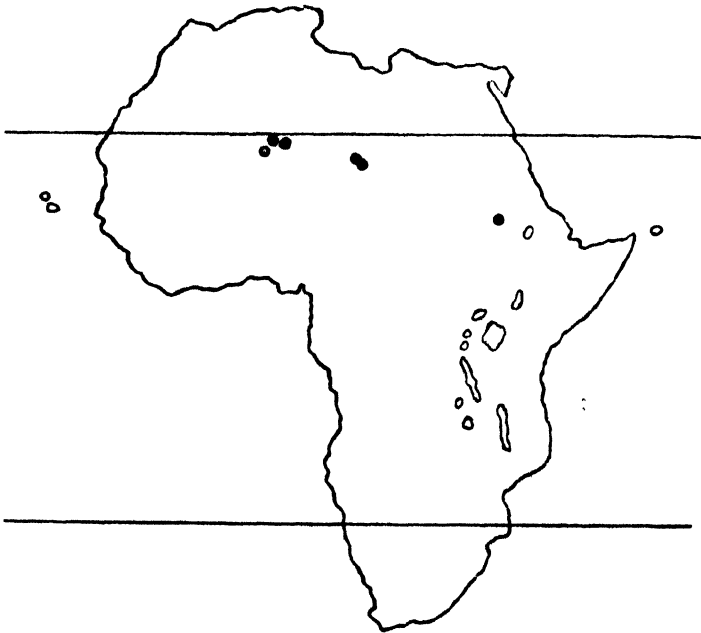


FIG. 8.—Distribution in Tropical Africa of *Potamogeton perfoliatus* L.

8. POTAMOGETON PERFOLIATUS L. Sp. Pl. i, 126 (1753). Battand. & Trab. in Bull. Soc. Bot. Franc. liii, Sess. Extraord. 23 (1907). Bonnet in Bull. Mus. Nation. Hist. Nat. xviii, 515 (1912); Hagstr. Crit. Res. 254, figs. 116 G-H, 117 A-O, 118 A (1916). Diels in Engl. Bot. Jahrb. liv, Beibl. 120, 63 (1917). Maire in Bull. Mus. Nation. Hist. Nat., sér. 2, iii, 522 (1931); in Mém. Soc. Hist. Nat. Afr. Nord, iii, 53 (1933); Contrib. Étud. Fl. Tibesti, 6 (1935); in Mém. Acad. Sci. Inst. Franc., sér. 2, lxii, 6 (1936).

ALGERIA. Territoires du Sud : Ahaggar, Tit, 1905, R. Chudeau (Alg, sterile).

FRENCH EQUATORIAL AFRICA. Tchad : Tibesti, Mt. Madigué, 1,200 m., 1931,

*M. Dalloni* (Alg, sterile). Tibesti, Enneri Abba near crater of Begour, 1,200 m., 1931, *M. Dalloni* (Alg, sterile).

ANGLO-EGYPTIAN SUDAN. Blue Nile Prov. : Ghubshan canal, 1936, *F. W. Andrews* A137 (K).

*P. perfoliatus* is widely distributed in Europe, northern Africa, Temperate Asia, and North America, and also occurs (perhaps adventively) in southern India and eastern Australia. It was originally described from Europe.

As an indigenous species in Tropical Africa *P. perfoliatus* appears to be restricted to the high mountain masses of the Sahara, to which it extends from western North Africa. I have seen specimens from Ahaggar and Tibesti, and according to Maire material has also been collected (by T. Monod, no. 281) at Tigheurt, in Tassili-ta-n-Adrar, to the south-west of Ahaggar.

During the last year *P. perfoliatus* has been found in a canal in the Blue Nile Province of the Anglo-Egyptian Sudan. This belated discovery in an artificial watercourse suggests that the species has recently been introduced into the region.

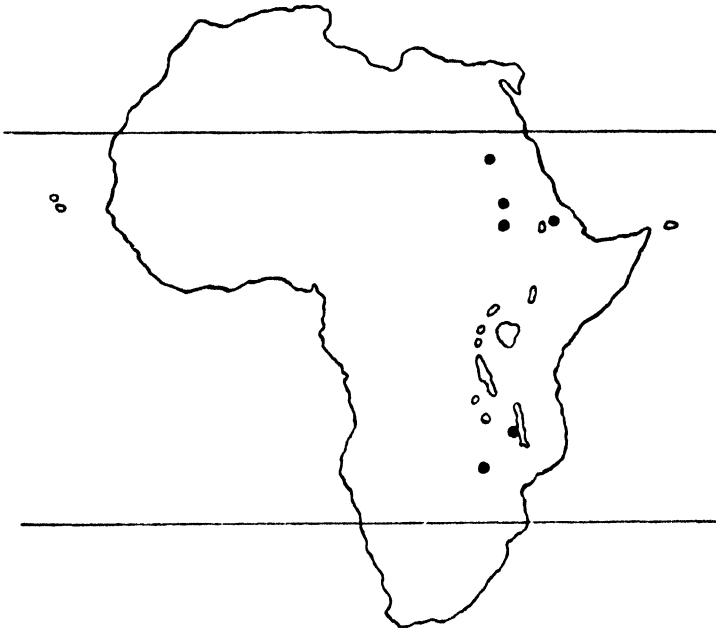


FIG. 9.—Distribution in Tropical Africa of *Potamogeton crispus* L.

#### Sect. IV. BATRACHOSERIS Irmisch.

9. *POTAMOGETON CRISPUS* L. Sp. Pl. i, 126 (1753). Solms in Schweinf. Beitr. Fl. Aethiop. i, 194 (1867). Aschers. & Schweinf. in Schweinf. tom. cit. 292 (1867). Dur. & Schinz, Consp. Fl. Afr. v, 493 (1894), pro parte. A. Benn. in Journ. of Bot. xxxiii, 137 (1895); in Dyer, Fl. Trop. Afr. viii, 221 (1901);

apud Rendle in Journ. Linn. Soc., Bot. xxxviii, 24 in obs. (1907). Broun, Cat. Sudan Flow. Pl. 86 (1906). Graebn. in Engl. Pflanzenr. iv, 11, 97, fig. 23 (1907). Engl. in Engl. & Drude, Veg. Erd. IX, ii, 95 (1908). Hagstr. Crit. Res. 58, figs. 21-22 (1916). Broun & Massey, Fl. Sudan, 367 (1929).

ANGLO-EGYPTIAN SUDAN. Khartoum Prov.: White Nile, Khartoum, near junction of White and Blue Niles, 1905, *A. F. & H. M. Broun* 631 (K). Kordofan Prov.: 1837-38, *C. G. T. Kotschy* 366 (K, sterile).

ABYSSINIA (*ex* Ascherson & Schweinfurth).

NYASALAND. West shore of L. Nyasa, Roangwa, 1861, *J. Kirk* (K).

SOUTHERN RHODESIA. Mashonaland: Lomagundi Distr., c. 1,050 m., 1921, *F. Eyles* 3142 (K, sterile; NHP, sterile).

This very distinct species has a wide Old World distribution in Europe, Africa\*, Asia, and Australia, and is also found in North America where it appears to have been introduced. It was originally described from Europe.

In Tropical Africa *P. crispus* is confined to the east and appears to be sporadic in its occurrence, for although it has been reported from regions as far apart as Halfa Province, in the northern Anglo-Egyptian Sudan, and Lomagundi District, in Southern Rhodesia, there are few records from the intervening area and none at all from the great lake systems of Kenya, Uganda, and Tanganyika Territory. Like *P. trichoides* it is a species to be looked for in East Africa.

A specimen of *P. crispus* collected by H. Steudner (no. 212) was cited by A. Bennett in the 'Flora of Tropical Africa' with the locality 'Bahr el Tussuf'. This specimen, which is in the Kew Herbarium, is not from Tropical Africa but from the Bahr Yusef, in El Faiyum, Egypt.

#### INDEX TO NUMBERED TROPICAL AFRICAN GATHERINGS EXAMINED.

- ANDREWS, F. W. (Anglo-Egyptian Sudan). A137, *perfoliatus*. A138, A142, *nodosus*. W12, *pectinatus*.  
 BAGSHAW, A. G. (Uganda). 703, *octandrus*. 954, *nodosus*.  
 BALFOUR, I. B. (Socotra). 2, 3, *nodosus*. 152 (or 650), *pectinatus*. 168, *nodosus*.  
 BARTER, C. (Niger Exped.). 1069, *octandrus*.  
 BAUM, H. (Kupene-Sambesi Exped.). 96, *octandrus*.  
 BEQUAERT, J. (Belgian Congo). 5312, *pectinatus*.  
 BLENKIRON, M. E. (Rhodesia). *Herb. C. E. Moss* 14860, *octandrus*. *Herb. C. E. Moss* 16406, *Schweinfurthii*.

\* South African material includes *P. crispus* var. *najadoides* Graebn. in Engl. Pflanzenr. iv, 11, 100 (1907). I have seen the following specimens of *P. crispus* from South Africa:—TRANSVAAL: *C. E. Moss* 13589 (BM); *W. Nelson* 70 (K); *F. Wilms* 1658 (BM; K). NATAL: *J. Medley Wood* 154 (K) and without no. (AM; BM, sterile); *J. Sanderson* 2018 (K); *R. Schlechter* 3122 (AM, sterile; BM; K, sterile). ORANGE FREE STATE: *J. W. Pont* 598 (NHP, sterile); *without collector* (NHP 21, sterile; NHP 22, sterile). CAPE PROVINCE: *M. E. Barker* 4 (K, sterile); *E. G. Bryant* 964 (K); *H. G. Flanagan* (NHP, sterile); *A. Parker* (NHP); *W. Tyson* 2125 (SAM 23678).

- BROUN, A. F. & H. M. (Anglo-Egyptian Sudan). 631, *crispus*.  
 BROWN, E. (Uganda). 223, *Schweinfurthii*. 333, *nodosus*.  
 BURTT, B. D. (Virunga Mts. and Tanganyika Territory). 3267, *pectinatus*. 3345, *Schweinfurthii*.  
 CHEVALIER, A. (Oubangui-Chari). 7856, *octandrus*.  
 CUNNINGTON, W. A. (African Lakes). 2, 8, *Schweinfurthii*. 12, 23, *pectinatus*. 45, *Schweinfurthii*. 54, *octandrus*. 56, *Schweinfurthii*.  
 DINTER, K. (South West Africa). 5254, *Schweinfurthii*. 7203, *octandrus*. 7241, *Schweinfurthii*.  
 DUMMER, R. A. (British E. Africa and Uganda). 1633, 2473, *nodosus*. 4577, *Schweinfurthii*.  
 EGGELING, W. J. (Uganda). 503, *nodosus*. E.1655, E.2227, *octandrus*. E.2233, *Schweinfurthii*.  
 EYLES, F. (Rhodesia). 36, *nodosus*. 655, *octandrus*. 659, *nodosus*. 3141, *panormitanus* and *trichoides*. 3142, *crispus*. 3161, *Schweinfurthii*. 5853, *octandrus*.  
 FRIES, R. E. (Uganda, Belgian Congo, and Rhodesia). 137, 655, *Schweinfurthii*. 691, *nodosus*. 1024, *octandrus*. 1582, 1742, 2000, *pectinatus*.  
 FRIES, R. E. & T. C. E. (Kenya). 1800, 2611, *nodosus*.  
 GIBBS, L. S. (Matopo Hills and Victoria Falls). 94, 146, *nodosus*. 190, *panormitanus*.  
 GILLET, J. B. (Abyssinia). 5467, *pectinatus*. 5471, *nodosus*.  
 GILLILAND, H. B. (S. Rhodesia). 63, 527.8, *nodosus*.  
 GOSSEWILER, J. (Angola). 1948, 8985, *octandrus*.  
 GRAHAM, M. (Kenya). H.47-28, *Schweinfurthii* [and *Vallisneria* sp.].  
 HAARER, A. E. (Tanganyika Territory). 2110, 2337, *nodosus*.  
 HANCOCK, G. L., & CHANDLER, P. C. (Uganda). 135, *nodosus*.  
 HAZEL, C. (Uganda). 226, *nodosus*.  
 HISLOP, A. (S. Rhodesia). Z.108, *octandrus*.  
 KOTSCHY, C. G. T. (Kordofan). 366, *crispus*.  
 LAWS (L. Nyasa). 3, *pectinatus*.  
 LE TESTU, G. (Oubangui-Chari). 3457, *octandrus*.  
 LIEBENBERG, L. C. C. (Uganda). 225, *Schweinfurthii*. 734, *octandrus*. 750, *Schweinfurthii*.  
 LINDER, D. H. (Uganda and Belgian Congo). 1922, *Schweinfurthii*. 2019, 2019a, *pectinatus*. 2590, *Schweinfurthii*. 2594, *nodosus*.  
 LYNES, H. (Darfur). 7, *panormitanus*.  
 MAIRE, R. (Sahara). 1226, *hoggarensis*.  
 MAITLAND, T. D. (Uganda). 367, *Schweinfurthii*.  
 NAPIER, E. R. (Kenya). 470, *Schweinfurthii*.  
 PREUSS, P. (British Cameroons). 451, *octandrus*.  
 QUARTIN-DILLON, R., & PETIT, A. (Abyssinia). 571, *panormitanus*.  
 RAND, R. F. (Mashonaland). 540, *nodosus*.  
 ROGERS, F. A. (S. Rhodesia). 5677, *nodosus*.  
 SCHIMPER, W. (Abyssinia). 135, *nodosus*. 179, 530, 570, *panormitanus*. 571, 958, *nodosus*. 1359, *Schweinfurthii*.  
 SCHINZ, H. (R. Cunene and Kalahari). 780, *pectinatus*. 1001, *octandrus*.  
 SCHOENFELDER, E. B. W. (South West Africa). 1008, *pectinatus*.  
 SCHWEINFURTH, G. A. (Bahr el Ghazal and Nianniam land). 1165, 1223, *Schweinfurthii*. 1225, 2909, *octandrus*.  
 SCHWEINFURTH, G. A., & RIVA, D. (Eritrea). 891, *nodosus*. 896, *panormitanus*. 2110, *Schweinfurthii*.  
 SIMPSON, N. D. (Anglo-Egyptian Sudan). 7183, *octandrus*. 7204a, 7204b, 7665, *Schweinfurthii*. 7701, *octandrus*.  
 SNOWDEN, J. D. (British E. Africa and Uganda). 607, *nodosus*. 1507, *nodosus* and *Schweinfurthii*. 1836, *panormitanus*.

- STAUDT, A. (British Cameroons). 462, *octandrus*.  
 STOLZ, A. (Kyimbila district). 2253, *pectinatus*. 2462, *nodorus*. 2649, *pectinatus*.  
 SWYNNERTON, M. F. S. (Gazaland). 958, *panormitanus*.  
 TAYLOR, G. (Kenya and Uganda). 1022, *nodorus*. 1594, *Schweinfurthii*. 1594a, 1595, *trichoides*. 2174, *nodorus*. 2336, *pectinatus*. 3326, *octandrus*. 3358a, *Schweinfurthii*.  
 TEAGUE, A. J. (S. Rhodesia). 571, *nodorus*.  
 THOMAS, A. S. (Uganda). 1210, *pectinatus*. 1211, *Schweinfurthii*. 1216, *trichoides*. 1226, *Schweinfurthii*.  
 TISSERANT, C. (Oubangui-Chari). 1420, *octandrus*.  
 VAN SON, G. (Vernay-Lang Kalahari Exped.). *Herb. Transv. Mus.* 28986, *octandrus*.  
 WELWITSCH, F. (Angola). 248, *octandrus*. 249, *nodorus*. 250, *pectinatus*.  
 WORTHINGTON, E. B. (Kenya and Uganda). 290.3, 711 in part, *pectinatus*.

## EXPLANATION OF THE PLATES.

## PLATE 21.

- A. *Potamogeton Schweinfurthii*. A flowering specimen from the Bahr el Ghazal, Anglo-Egyptian Sudan, with coriaceous floating upper leaves. All the leaves have more or less elongated petioles. The specimen is the lectotype of the species, *Schweinfurth* 1223 (sheet 1) in *Herb. Kew*.  
 B. *Potamogeton Schweinfurthii*. Flowering material from a pond in Kenya, with all the leaves submersed and subsessile. The sheet is *Taylor* 1594 in the British Museum Herbarium.

## PLATE 22.

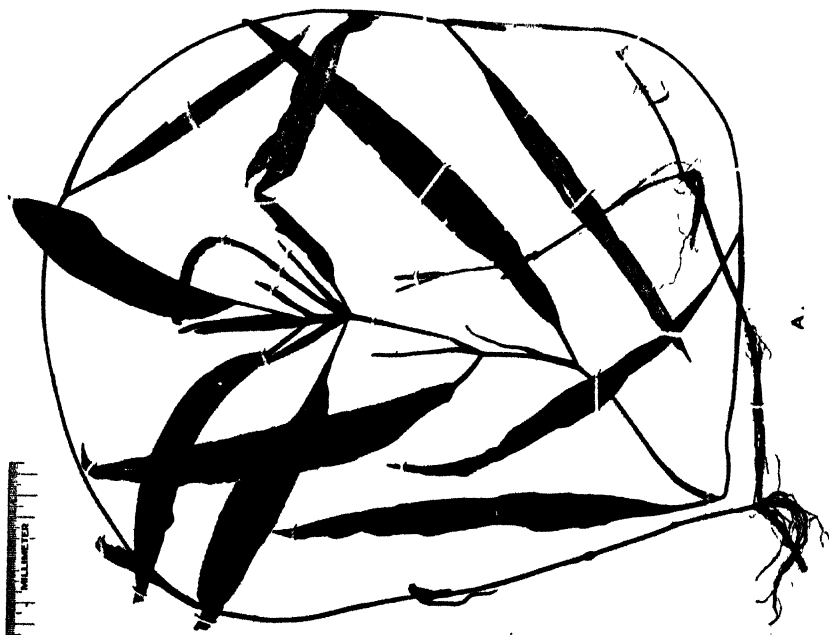
- A. *Potamogeton Schweinfurthii*. A flowering specimen from Lake Nyasa, with the upper leaves intermediate ('semi-floating') in character. All the leaves are distinctly petiolate. The sheet is *Cunnington* 2 in the British Museum Herbarium.  
 B. *Potamogeton Schweinfurthii*. Sterile (apparently juvenile) material from Lake Bangweulu, in Northern Rhodesia, with all the leaves small, narrow, and submersed. The material is *Fries* 655 in the herbarium of the Universitetets Botaniska Museum, Uppsala, and is the type of *P. repens* Hagstr.



BANDY







A.



B.



Further Notes on the Genera *Fumaria* and *Rupicapnos*.—IV.

By H. W. PUGSLEY, B.A., F.L.S.

(PLATES 23 &amp; 24)

[Read 21 January 1937]

WHEN the third Supplement to the 'Revision of the Genera *Fumaria* and *Rupicapnos*' was published in the Journal of this Society in 1934, it was anticipated that but few new forms remained to be described. This expectation has not been fulfilled, for five further species of *Fumaria*, and four of *Rupicapnos*, have since been brought to light in Morocco, and one new *Fumaria* in Palestine. Interesting forms have also been observed in the herbaria at Berlin and Munich.

The exploration of Morocco in recent years, as narrated by Professors Emberger and Maire in 'Mémoires de la Société des Sciences Naturelles du Maroc', xxxviii (1934), forms a fascinating story of botanical adventures that can never be repeated in any region near Western Europe. Up to nearly 1920, Morocco was practically a forbidden country for Europeans, and very little was known of its interior and its flora, except for the districts bordering on the Atlantic and the way thence to Marrakech, which had been visited in 1871 by Hooker, Ball and Maw. But during the last fifteen years numerous botanists have made incursions into the country on all sides. Dr. Maire has explored nearly every district, the Moyen and the Great Atlas, the Sous and the Anti-Atlas stretching southwards to the Sahara, and the Eastern Riff country now administered by Spain. The excursions of M. Jahandiez have been almost as ubiquitous. M. Humbert has specialized in the south-east regions that are approached from Southern Algeria. MM. Emberger and de Litardière have traversed the interior in various directions, especially in the Great Atlas, and Dr. Font-Quer has done notable work in the Riffian Atlas, where M. Faure also has made important discoveries. But the country is so mountainous and difficult of access that, with all the work that has been accomplished, some plants gathered by the earlier collectors have not yet been re-found, and many more species of its rich and varied flora probably still await discovery. Among the *Fumariae*, while *F. Ballii* Pugsl. and *F. Munbyi* Boiss. & Reut. are now well represented in herbaria, more and better material of *F. Embergeri* Pugsl., *F. berberica* Pugsl., *F. maurorum* Maire, and *F. Schrammii* var. *Pugsleyana* Maire is still a desideratum.

The opening up of Morocco reveals the fact that in no country of the world are so many species of *Fumaria* to be found. In 1917, when the Revision was written, twelve Moroccan species (8 *Grandiflorae* and 4 *Parviflorae*) were

known, in comparison with fourteen (10 *Grandiflorae* and 4 *Parviflorae*) in Algeria. At that date Spain was credited with the largest number of species, i.e. seventeen (11 *Grandiflorae* and 6 *Parviflorae*). At the present time, with the additions in this paper, twenty-one species of *Grandiflorae* and nine of *Parviflorae* are known for Morocco, as against fourteen and seven respectively for Algeria, and thirteen and seven for Spain.

Of the new Moroccan species here described we owe four, two in each genus, to M. Emberger, one in each genus to Dr. Maire, and a fourth *Fumaria* to Frère Sennen, while a fifth, obtained by the native collector, Ibrahim, in 1888, was detected in the herbarium at Berlin and has been lent for examination through the kindness of Professor Diels. The sixth *Fumaria* was discovered near Haifa, in Palestine, by Herr A. Bertschinger, and is the first addition to the Asiatic species of the genus since the publication of Haussknecht's *F. cilicica* and *F. Boissieri* in 1873 (excepting *F. indica* Pugsl., raised from previous varietal rank). The fourth new *Rupicapnos*, apparently the finest in the genus, was obtained by Herr Erik Wall near Taza, in which neighbourhood other species have already been found.

The method and sequence here adopted follow those of the Revision and its earlier Supplements, with similarly constructed descriptions of new groups and italicised chief contrasting characters.

## FUMARIA.

### SECTIO I. GRANDIFLORA.

In the Sectional diagnosis '*F. micranthifolia*' should be inserted after '*F. Ballii*'.

### SUBSECTIO I. AGRARIAE.

#### Series Eu-Agrariae.

#### 1. *FUMARIA AGRARIA* Lagasca.

The variety *elata* was described in J. Ball's '*Spicilegium Florae Maroccanae*' in Journ. Linn. Soc. xvi, 315 (1878) as '*var. elata* an *F. rupestris* var. *laxa* Boiss. In rupibus calcareis prope Tetuan, Shedma, prope Marocco . . . var. nostra differt a typo sepalis longius acuminatis apice subherbaceis, fructu insigniter compresso et carinato'. In Herb. Berol. there are authentic sheets of this plant, received from Ball, from Tetuan and Marocco. The specimen from Tetuan is annotated by Ball '*A form of F. agraria* (v. *elata* nob.—sepals longer, acuminate, subvirescent) approaching *F. rupestris* Boiss.'. The plant has both good flowers and fruits; the corolla is 13.5 mm. long, with narrowly lanceolate, subentire sepals exceeding 4 mm.; the fruit is that of typical *F. agraria*, from which the specimen seems indistinguishable. The Marocco *exsiccata*, also in good condition, is different. Its corollas are much smaller (about 11 mm. long), and less broadly winged, but with similar long, narrow sepals. The capsules are

of *agraria* form, but relatively small. The plant appears to be a weak or shade-grown example of ordinary *F. agraria*. There thus seems little ground, judging from these specimens, for retaining the variety *elata*. There is also in Herb. Berol. an example of *F. agraria* from Agadir, and another sheet from Casablanca, containing both the typical species and var. *chilensis* Parl., Ball remarking on the label 'fruit very apiculate or almost quite blunt growing together'.

An interesting form recently received, collected by Dr. Maire in April 1936, near Cap Ghir, in south-west Morocco, seems to constitute a distinct variety, thus :—

ε. *tigertensis*, var. nov.

*Exsicc.* Maire, Iter Marocc. xxvi, Tigert prope Cap Ghir, 1936 (typus in Hb. Pugsley) !

*Planta habitu laxo, verisimiliter haud scandens. Racemi densiusculi, sub-20-flori. Sepala 3.5–4 mm. longa, sub 2 mm. lata, ovato-lanceolata vel lanceolata, longe acuminata. Corolla 11–12 mm. longa, praeter petalorum interiorum apicem atropurpureum alba, vel apice tandem leviter roseo-tincta. Fructûs relative parvi, 2–2.25 mm. longi, 2.25–2.5 mm. lati, subrotundo-quadrati, subtruncati ut in var. *erostatrâ*, per styli basin breviter sed plane apiculati. Aliter ut in typo.*

#### 4. FUMARIA RUPESTRIS Boissier & Reuter.

This species has been found to occur in the Anti-Atlas Occidental of Morocco, a great southern extension of its range. A form near the type was obtained by M. Emberger in 1934 near Tiznit, and the variety *pallescens* Pugsley at Suck el Arba du Sahel.

Dr. Maire has kindly sent one of Battandier's original specimens from the Plaine des Issers of *F. rupestris* var. *robusta*, published in Battandier and Trabut's 'Flore d'Algérie', i, 27 (1888), with *F. arundana* Boiss. shown as a synonym. The specimen is not a form of *F. rupestris*, but is *F. atlantica* Coss. & Dur. var. *platyptera* Pugsley.

An interesting form was collected in 1914 at Ito, in the Middle Atlas (1,400 m. alt.). This has large flowers like the Ronda variety *laxa* Boiss. & Reut., but its bracts are broad and the sepals ovate. The material seen lacks fruit, but the plant is probably at least varietally distinct. In 1936 Mr. N. D. Simpson collected the variety *laxa* by a roadside at Fez. His specimen (Simpson no. 36130 !) closely resembles the Ronda plant.

#### 4 c. FUMARIA IFRANENSIS, sp. nov. (Pl. 23, fig. 1.)

*Exsicc.* Emberger, Ifrane, in Atlante medio (Morocco). 27. 5. 31 (typus in Hb. Pugsley) !

*Fumaria habitu robusto, laxo, petiolis cirrhosis scandens. Folia viridia, foliolis in lobos oblongos vel lanceolatos, plus minusve acutos saepe mucronatos fissis irregulariter 2–3-pinnatisecta. Racemi longi, laxiusculi, multiflori (ad 20-flori), pedunculos breves longe superantes. Bractee lineari-oblongae,*

acuminatae, *pedicellis* fructiferis *suberectis* circa 4 mm. longis apice incrassatis paulo breviores. *Sepala* circa 3 mm. longa, 1.5 mm. lata, oblonga, peltata, carinâ excurrente valde acuminata, leviter *dentata*, praeter nervum dorsalem viridiusculum albida, in fructu nonnunquam persistentia. *Corolla* 10–11 mm. longa, albida, dorso paullulum roseo-tincta, haud angusta; *petalo superiore subacuto*, calcare recto breviusculo alisque atropurpureis apicem attingentibus carinam subaequantibus praedito; *petalo inferiore marginibus angustis* albidis *patentibus* acuto; *petalis* interioribus apice sursum curvatis atropurpureis. *Fructus mediocres*, 2–2.25 mm. longi, 2.25–2.5 mm. lati, *subrotundo-obovati*, *obtusiusculi*, styli basi brevissime mucronati, paulo compressi sed plane carinati, inferne multo angustati, in sicco apicis foveolis angustis nigricantibus dense sed tenuiter *tuberculato-rugosi*.

Haec species *F. rupestri* Boiss. & Reut. valde affinis est, sed per habitum robustum, per sepala minora et per corollam albidam haud angustam satis differt. *F. Embergeri* Pugsl. floribus majoribus cum petali superioris alis albidis, sepalis minimis et fructibus rostratis facile distinguitur. *F. multiflora* Pugsl. propter racemos etiam longiores, corollas majores graciles alis albidis praeditas, atque fructûs ovatos acutiusculos diversa est. *F. agraria* Lag. florum majorum alis albidis, sepalis angustis diu persistentibus, et fructûs valde compressi carinâ in rostrum emarginatum productâ longe distat.

*F. ifranensis* prope Ifrane in Atlante medio Mauritaniae crescit.

This plant, alluded to in the second Supplement to the Revision (Journ. Linn. Soc., Bot. xlix, 95 (1932)), is evidently closely allied to *F. rupestris* Boiss. & Reut. and was at first thought to be a variety of that species. But on further examination, although its fruit is scarcely separable from that of *F. rupestris*, except for the narrower, black apical pits, yet the corolla seems essentially distinct both in form and colour. In a considerable series of exsiccatae, mostly from North Africa but partly from Spain, the very narrow corolla of *F. rupestris*, slightly winged and with long, deflexed spur, is notable throughout, though less marked in the variety *laxa* and the form mentioned above as growing at Ito. M. Emberger's specimen of the Ifrane plant consists of branches taken from a luxuriant, lax-growing individual, and shows numerous long racemes, from which unfortunately most of the flowers have fallen. But the remaining corollas appear normal and sufficient to justify the description of the plant as a new species distinct from *F. rupestris*. It seems best placed after *F. rupestris* and *F. Embergeri* in the Series *Eu-Agrariae*.

##### 5. *FUMARIA BALLII* Pugsley.

There are two examples of this species in Herb. Berol. (ex Herb. Cosson). One, from Argakaoubagh and Mt. Omahra, north-east of Hazeroualt, south-west Morocco, collected by Mardochee in 1876, is fairly typical. The other, gathered by Ibrahim in 1884 between Mogadore and Marrakech, has bracts longer and fruits smoother than those of Ball's original plant at Kew, but otherwise it is similar. Excellent specimens, with good foliage and flowers, were collected at Marrakech in 1934 by Mr. A. W. Trethewy.



Another form of this species was discovered in 1934 by M. Emberger at Tiznit, in the Sous district of south-west Morocco, which differs considerably from the type in the form of its fruit. The capsules are very shortly beaked and much more distinctly keeled, and so approach the form seen in *F. agraria* and *F. rupestris*; but the plant possesses the finely dissected foliage and the flowers of *F. Ballii*, and appears to be best regarded as a new variety of that plant, thus:—

*β. tiznitensis*, var. nov.

*Exsicc.* Emberger, Sous; terrains vagues à Tiznit; 25. 4. 34 (typus in Hb. Pugsley)!

Planta bracteis pedicellis breviores (3–4 mm. longos) apice incrassatos fere aequantibus, fructibusque sine mucrone 2–2.25 mm. longis, 2.25–2.5 mm. latis, plane carinatis, obtusissimis, brevissime mucronatis, inferne parum angustatis, siccitate obscurius tuberculato-rugosis praedita. Aliter ut in typo.

*F. Ballii* has also been collected in the Riffian Atlas (Sennen and Mauricio, Metalza, Dar Drius, 1934, as *F. agraria*!). The plant, as seen in Herb. Mus. Brit., is typical, except that the fruit is rather broad and shortly beaked, and so intermediate between that of the type and var. *tiznitensis*.

5 a. *FUMARIA MICRANTHIFOLIA*, sp. nov. (Pl. 23, fig. 2.)

*Exsicc.* Maire, Inter Oued Zem et Christian (900 m.), 16. 4. 34 (typus in Hb. Pugsley)!

*Fumaria habitu satis robusto*, e basi valde ramosa. *Folia* virentia, foliolis in lacinias parvas planas anguste oblongas acutas vel mucronatas fissis 3–4-pinnatisecta. *Racemi* laxi, multiflori (10–20-flori), *pedunculos* crassos brevissimos longe superantes vel fere subsessiles. *Bractae* angustae, lineares, tenuiter acuminatae, *pedicellis* fructiferis suberectis circa 5 mm. longis apice incrassatis tertiâ parte breviores. *Sepala* 3 mm. longa, 1–1.5 mm. lata, oblonga vel lanceolata, vix peltata, acuminata, obscure dentata, nervo dorsali lato viridiusculo albida, verisimiliter facile caduca. *Corolla* 11–12 mm. longa, albida, satis angusta; *petalo superiore obtuso*, calcare curvato longiusculo et *alis albidis* sursum reflexis carinam superantibus apicemque attingentibus praedito; *petalo inferiore* obtusiusculo *marginibus paulo angustis patentibus* apicem fere attingentibus; *petalis* interioribus apice sursum curvatis atropurpureis. *Fructûs magni*, 2.75–3 mm. longi ac lati. *subrotundo-quadrati*, obscure *rostrato-subacuti*, parum compressi sed *conspicue* (praesertim basin apicemque versus) *carinati*, inferne breviter angustati, siccitate apicis foveolis obscuris dense tuberculato-rugosi.

*F. micranthifolia*, cum *F. Ballii*, per folia decomposita eis *F. micranthae* Lag. subsimilia, inter Subsectionis *Agrariarum* affines notabilis est. *F. Ballii* floribus roseis longioribus, sepalis minimis, fructibus formae omnino diversae minoribus facile separari potest. *F. rupestris*, praeter foliorum differentiam, floribus angustioribus plus minusve roseis, sepalis longioribus, fructibusque minoribus distinguitur; *F. Embergeri* per sepala minora, corollas longiores, fructûsque minores magis rostratos; *F. ifranensis* propter petali superioris alas

atropurpureas et fructûs minores apice nigricantes. *F. multiflora* florum plane longiorum angustiorum racemis etiam longioribus, fructibusque ovatis acutiusculis leviter rugosis, atque *F. agraria* sepalis angustis diu persistentibus, corollis majoribus, fructibusque retuso-rostratis separandae sunt.

*F. micranthifolia* fissuras rupium arenacearum inter Oued Zem et Christian (900 m. alt.) in Atlante Medio Occidentali Mauritaniae habitat.

This Fumitory, like *F. Ballii*, is remarkable for its combination of the finely cut foliage characteristic of the Section *Parviflora* with the large flowers and fruits of the *Agrariae*. Its lax, nearly sessile racemes and large *rupestris*-like fruits are very conspicuous. From its aggregate of characters it may be held approximately intermediate between *F. Ballii* and *F. rupestris*, and it seems best placed in the Series *Eu-Agrariae* adjacent to the former.

#### Series Orientales.

8 a. *FUMARIA UNDULATA*, sp. nov. (Pl. 23, fig. 3.)

*Exsicc.* Emberger, Kerdous, Anti-Atlas ; 28. 4. 34 (typus in Hb. Instit. Scient. Chérifien et in Hb. Pugsley) !

*Fumaria* verisimiliter habitu satis robusto, petiolis cirrhosis scandens. *Folia* irregulariter 2-3-pinnatisecta, foliolis in lobos subellipticos vel oblongos acutos vel mucronatos fissis praedita. *Racemi* (in exemplaribus visis) *laxiusculi*, *pauciflori* (sub-10-flori), *pedunculos* mediocres *subaequantes*. *Bractee* lineari-lanceolatae, acuminatae, *pedicellis* fructiferis *suberectis* breviusculis (circa 3 mm. longis) apice satis incrassatis fere *aequilongae*. *Sepala* 3.5-4 mm. longa, circa 2 mm. lata, anguste ovata vel oblonga, carinâ excurrente longe cuspidata, inferne irregulariter dentata vel laciniata, praeter nervum dorsalem rubicundum albida, in fructu juniore persistentia. *Corolla* circa 11 mm. longa, rosea, haud angusta ; *petalo superiore* alis purpureis undulato-crenatis sursum reflexis carinam superantibus apicemque attingentibus obtusiusculo ; *petalo inferiore* marginibus latiusculis roseis crenatis patulis apicem fere attingentibus subacuto subspathulato ; *petalis* interioribus apice sursum curvatis purpureis. *Fructûs*, ut videtur, *modici*, 2 mm. longi et 2.25 mm. lati, late subrotundo-obovati, verisimiliter sine mucrone obtusissimi, satis carinati sed paullulum compressi, siccitate apicis foveolis latis obscuris leviter tuberculato-rugosi.

*F. undulata*, e speciminibus paucis descripta, ad Subsectionem *Agrariarum* certe pertinet, et propter fructûs verisimiliter omnino obtusos ad Seriem *Orientalium* forsitan referenda sit. Ab hujus seriei alis speciebus per flores roseos apice purpureos statim separanda est. Primo intuitu *F. rupestris* refert, sed haec non modo per fructûs subrostratos sed etiam corollâ angustiore petalorum exteriorum alis angustis nec undulato-crenatis plane distat.

*F. major* Bad. et *F. Gaillardotii* Boiss. per corollas majores apice atropurpureas, sepalâ latiora, fructûsque majores plus minusve mucronatos facile distinguuntur.

*F. undulata* in solo siliceo prope Kerdous (1,200 m. alt.) in Anti-Atlante Mauritaniae australis crescit,

This new species, discovered in 1934 by M. Emberger in the extreme south of Morocco, has been described from the very limited material available, because its discoverer does not expect to refine it immediately. At first sight it recalls *F. rupestris*, but the corolla is much broader than in that species, with the two outer petals apically dilated into distinctly waved or crenate wings and margins. The fruit, so far as can be judged, is entirely obtuse, and more like that of *F. judaica* Boiss. or *F. amarysia* Boiss. & Heldr. than any other species among the *Agrariae*.

9. *FUMARIA JUDAICA* Boissier.

This species is now known from Mt. Athos, Macedonia (Hill, Sandwith and Turrill, 1934, no. 2470 !).

10. *FUMARIA AMARYSIA* Boissier & Heldreich.

There is a specimen of this local plant in Herb. Berol. collected by Heldreich in 1898 in the island of Chios (Cyclades).

11. *FUMARIA MACROCARPA* Parlatores.

This occurs at Mt. Athos (Hill, Sandwith and Turrill, 1934, no. 2289 !).

SUBSECTIO II. *CAPREOLATAE*.

Series *Eu-Capreolatae*.

12. *FUMARIA CAPREOLATA* Linn.

There is a specimen of this plant in Herb. Reg. Monacense from Monte Video (Herter, 1925 !). The variety *albiflora* Hamm., which is perhaps the only form of the species occurring in the Balkan Peninsula, grows at Mt. Athos (Hill, Sandwith and Turrill, 1934, no. 2271 !).

13. *FUMARIA FLABELLATA* Gasparrini.

This species was collected at Mt. Athos in 1934 (Hill, Sandwith and Turrill, no. 2636 !).

14 a. *FUMARIA MELILLAICA*, sp. nov. (Pl. 23, fig. 4.)

*Exsicc.* Sennen, no. 7498, Gurugu, vers Basbel (Ker-Ker), 1933, non 1930, 1931, 1932, 1934, as *F. capreolata* var. *Guruguensis* (typus in Hb. Mus. Brit.) !

*Fumaria habitu gracili*, internodis longis elongata petiolisque cirrhosis scandens. *Folia* irregulariter 2-pinnatisecta, foliolis in lobos plerumque latos ellipticos, obtusos saepe mucronatos fissis, infimis breviuscule petiolatis praedita. *Racemi densiusculi, multi*-(sub-20)-*flori, pedunculis* plus minusve longis primarii breviores, reliqui *subaequilongi*. *Bractae* albae, lineari-lanceolatae, acuminatae, *pedicellis* fructiferis arcuato-recurvatis apice valde incrassatis paulo breviores. *Sepala* 3-4 mm. longa, 2-2.25 mm. lata, ovata, peltata, breviter acuminata vel acuta, plus minusve dentata vel basi laciniata, nervo dorsali viridiusculo alba, *Corolla* mediocris, 9-11 mm. longa, pallida rosea; petalo

*superiore* satis angusto *alis atropurpureis* sursum reflexis carinam haud aequantibus apicemque vix attingentibus *subacuto*, calcareque adscendente rotundato; *petalo inferiore marginibus* roseis angustis *suberectis* apicem haud attingentibus acuto; *petalis* interioribus apice sursum curvatis atropurpureis. *Fructūs parvi*, circa 2 mm. longi et 1.75 mm. lati, *ovali-subrotundi*, *obtusissimi*, paullulum compresso-carinati, siccitate apicis foveolis latis dense sed haud grosse *rugosi*.

Haec species per pedunculos longos, pedicellos arcuato-recurvatos apice valde dilatatos, sepalaque magna ad Subsectionem *Capreolatarum* (Series *Eu-Capreolatae*) sine dubio pertinet. *F. capreolata*, *F. Normanii* Pugsl. et *F. purpurea* Pugsl. floribus majoribus fructibusque relative laevibus plane differunt. *F. flabellata* floribus albis multo majoribus, petali inferioris marginibus patulis, fructibusque majusculis distinguitur; *F. dubia* Pugsl. floribus longioribus fructibusque obovatis subacutis certe diversa est. *F. praetermissa* Pugsl. et *F. coccinea* Lowe ex Pugsl., Seriei *Macrosepalarum*, quamvis pedicellis suberectis nec recurvatis, *F. melillaica* aliquanto referunt, attamen *F. praetermissa* bracteis longissimis fructibusque subretusis, et *F. coccinea* floribus angustis rubris facile distinguendae sunt.

*F. melillaica* in collibus lapidosis in Gurugu, Basbel (Ker-Ker) versus (850 m. alt.), prope Melillam Mauritaniae Rifanae invenitur.

Under no. 7498, specimens from Gurugu, labelled *F. capreolata* var. *Guruguensis*, were sent out by Frère Sennen in five successive years. The plants for 1930 and 1931, as received in Herb. Mus. Brit., are weak examples of *F. capreolata*; that for 1932 is inseparable from *F. capreolata* var. *albiflora* Hamm., as pointed out in Journ. Linn. Soc., Bot., xlix, 518 (1934). The 1933 gathering is shown by its subrotund, rugose fruits to belong to a plant specifically distinct from *F. capreolata*, which is here described as a new species. The set for 1934 is typical *F. capreolata*. It would seem that the new species and *F. capreolata* grow in company.

#### Series **Macrosepalae**.

#### 15. **FUMARIA MACROSEPALA** Boissier.

There is fairly good material of *F. malacitana* Haussk. & Fritze in Herb. Berol. from the Sierra Nevada, named by Haussknecht himself, as well as an indifferent example of the type-gathering from Malaga. The plant is evidently very closely allied to *F. macrosepala* var. *obscura* Pugsl., for its sepals are distinctly smaller than in the typical species. But it shows rather more floriferous racemes than any other form of *F. macrosepala* that has been examined, and its fruit not only lacks the characteristic apiculus but differs appreciably in shape, being more compressed and ovate in profile. It thus seems desirable to recognise *F. malacitana* as a separate variety of *F. macrosepala*:—

*γ. malacitana* (Haussk. & Fritze), var. nov.

*F. malacitana* Haussk. & Fritze in *Flora*, lvi, 548 (1873).

Planta racemis densiusculis ad 14-floris bracteisque pedicellos fructiferos

breves saepe superantibus. Sepala 4-5 mm. longa, circa 3 mm. lata, late ovata. Corolla 10-11 mm. longa. Fructûs 2.5-3 mm. longi, 2.25-2.5 mm. lati, ovati, obtusiusculi, haud apiculati, quam in typo magis compressi. Aliter ut in typo.

This variety has not been observed among recent Spanish gatherings.

16 a. *FUMARIA PRAETERMISSA* Pugsley.

This species was collected by Mr. Trethewy in 1933 at Santa Cruz, in the island of Teneriffe—a further extension of its range in the Canaries. The specimen has laxer racemes than those previously seen, and fruits more distinctly ‘apice retusi’.

SUBSECTIO III. **MURALES.**

Series **Sub-Agrariae.**

18. *FUMARIA BICOLOR* Sommier.

There is a specimen of this plant in Herb. Berol. (H. C. Bolle, 1865, as *F. flabellata* !) from the island of Palmarola, off the Italian coast near Terracina. The species is now known from numerous maritime localities extending from the French Riviera along the West Coast of Italy to Malta and Algeria, as well as from Corsica and Minorca, but it has not yet been discovered on the Mediterranean coast of Spain or in Sardinia.

19. *FUMARIA BASTARDII* Boreau.

Examples of this species, collected in 1934 at Ghazir and Djounieh, in the Syrian Lebanon, have been received from Dr. Huber. They are the first specimens seen from Asia. Their flowers are too depauperate to be characteristic, but their fruits are small and subacute as in var. *vagans* (Jord.) Pugsley, and they are probably referable to this variety.

The variety *benedicta* (Nicotra) Pugsley was collected at Solero, in Corsica, by Dr. Aellen in 1935.

Series **Eu-Murales.**

21 a. *FUMARIA OUEZZANENSIS* Pugsley.

In 1934 this fine species was discovered by Herr Erik Wall in a new station, Sidi al Dallah, south-west of Taza. His specimen shows more broadly winged lower petals than those previously seen.

23. *FUMARIA MURALIS* Sonder.

There is a specimen of this species in Herb. Reg. Monacense, collected in 1817 at Windmill Hill, Gibraltar, and another from Montevideo (Herter, 1925 !). It also occurs at Swinemunde, Pomerania (Herb. Berger !). A second example from the Riffian Atlas of Morocco (var. *Loweii* Pugsley) is ‘Sennen & Mauricio, Beni-Sidel, Segangen, Falaises de Atlaten, 1934, as *F. capreolata*’ !

24. *FUMARIA APICULATA* Lange.

A form of this, with rather small sepals but otherwise fairly typical, was collected by M. Emberger in 1933 in the Controller's garden at Oulmès, south-west of Meknès. This is the first example of the species received from Morocco, excepting the variety *africana* Pugsl. of the Riffian Atlas.

## Series Sub-Latisepalae.

25. *FUMARIA PETTERI* Reichenbach.

Subsp. *Thuretii* (Boissier) var. *pikermiana* (Boiss.) Pugsl.

Dr. Rechinger collected this variety on the island of Seyros in 1927, and in Samos, Lesbos, and Ikaria in 1934. It was also found in 1934 at Mt. Athos (Hill, Sandwith and Turrill, no. 2393 !). In 1935 it was obtained at Smyrna by Herr Erik Wall.

27. *FUMARIA REUTERI* Boissier.

This species has now been found in the Riffian Atlas of Morocco. There are specimens in Herb. Mus. Brit. from Targuist (Sennen and Mauricio, 1933, as *F. apiculata* !) and from Ketama (Sennen and Mauricio, 1934, as *F. apiculata* !). In Sennen and Mauricio's 'Catalogo de la Flora de Rif Oriental', pp. 4, 5 (1933), both *F. Reuteri* and *F. apiculata* are given for Targuist, but no material of the latter species has been seen from this station.

## SECTIO II. PARVIFLORA.

## SUBSECTIO IV. LATISEPALAE.

29 b. *FUMARIA OBTUSISEPALA*, sp. nov. (Pl. 23, fig. 5.)

*Exsicc.* Ibrahim, Oum Djerid, Morocco, 20. 6. 88 (Hb. Cosson ut *F. parviflora*) (typus in Hb. Berol.) !

*Fumaria habitu satis gracili*, valde ramosa, verisimiliter haud scandens. *Folia* 2-3-(-4 ?-) *pinnatisecta*, foliolis in *lacinias planas lineari-oblongas* acutiusculas nonnunquam breviter mucronatas fissis praedita. *Racemi laxiusculi*, tandem elongati, 10-15-flori, *pedunculos brevissimos longe superantes* vel etiam subsessiles. *Bractae latae, oblongae, obtusae* vel mucronatae, albae, *pedicellis* fructiferis *erecto-patentibus, brevissimis* (2-2.5 mm. longis), apice conspicue incrassatis paulo breviores. *Sepala* 3-3.5 mm. longa, 1-1.5 mm. lata, *anguste oblonga, peltata, obtusa et plus minusve cucullata, irregulariter dentata*, nervo dorsali latissimo viridiusculo roseo-tincta. *Corolla parva, 5-6 mm. longa, rosea*; *petalo superiore obtusiusculo alis roseis carinam subaequantibus apicemque attingentibus atque calcare recto mediocri*; *petalo inferiore marginibus angustis roseis acutiusculo subspathulato*; *petalis interioribus apice purpureis. Fructus modici*, circa 2 mm. longi ac lati, *subrotundo-ovati, subacuti et brevissime apiculati*, parum compressi sed satis carinati, siccitate apicis foveolis parvis distinctis dense sed haud grosse rugosi.

*F. obtusisepala* propter foliorum lacinias angustas, bracteas magnas, floresque parvos sepalis maximis praeditos ad Subsectionem *Latisepalarum* referenda est. Ob sepalorum formam *F. Kralikii* Jord. refert, sed haec habitu etiam graciliore, pedicellis arcuato-recurvatis fructibusque minimis longe distat. *F. obtusisepalae* sepala longa etiam eis *F. mirabilis* Pugs. (formae typicae) subsimilia sunt, sed haec species per racemos densiores, corollas majores pallidiores petalorum interiorum apice atropurpureo praeditas, fructûsque majores rotundatos obtusissimos facile distinguitur. *F. micrantha* Lag. sepalis latioribus fructibusque semper sine apiculo separatur; *F. bracteosa* Pomel etiam racemis densis, foliorumque laciniis setaceis.

*F. obtusisepala* Oum Djerid in Mauritaniâ habitat.

This Fumitory, found during one of Ibrahim's plant-collecting expeditions for Cosson, seems never to have been subsequently noticed. Its sepals, which in form resemble those of *F. Kralikii* Jord., appear to be not only obtuse, but curiously hooded.

### 31. FUMARIA BRACTEOSA Pomel.

A plant collected by M. Faure in 1933 in cultivated ground at Delmonte, near Oran, has the aspect of a hybrid, *F. bracteosa*  $\times$  *parviflora* Lamk. Its habit is that of a vigorous *F. bracteosa*, with lax, somewhat intermediate foliage, and short, subsessile racemes of minute, white flowers. The capsules are only partially developed and very few contain perfect seeds.

## SUBSECTIO V. OFFICINALES.

### 34. FUMARIA CILICICA Haussknecht.

A specimen of this rare plant, collected by Miss O. Tufnell at the Cilician Gates, in Asia Minor, in 1933, has been sent to Kew. It is the only recent example that has been seen in herbaria.

## SUBSECTIO VI. MICROSEPALAE.

### Series Ambiguae.

### 38 a. FUMARIA ALGERIENSIS Pugsley.

The Herbarium at Berlin possesses a specimen of this plant, collected by Bavry at the Roman ruins of Lambessa, which is not far from the original similar station at Timgad.

### Series Eu-Microsepalae.

### 41. FUMARIA MICROCARPA Boissier ex Haussknecht.

There is a specimen of this rare species in Herb. Reg. Monacense from Georgia Caucasica (M. Wagner, as *F. Vaillantii* !), and another in Herb. Berol. from Novotshirkassk, in South Russia (Jakoushev, 1910, as *F. Schleicheri* !).

42 a. *FUMARIA MINIMA*, sp. nov. (Pl. 23, fig. 6.)

*Exsicc.* Bertschinger, Haifa, 1935 (typus in Hb. Pugsley) !

*Fumaria humilis* (in speciminibus visis 10 cm. alta), *gracilis*, satis ramosa, haud scandens. *Folia* plus minusve glauca, foliolis in *lacinias minimas lineari-oblongas acutas verisimiliter planas fissis 3-pinnatisecta*. *Racemi floriferi densi, pauciflori* (6–12-flori), *fructiferi elongati*, graciles, plerumque *sessilibus*. *Bractae lanceolatae, longe acuminatae, albae, pedicellis fructiferis erecto-patentibus brevissimis* (circa 1 mm. longis) apice ipso conspicue *incrassatis subduplo longiores*. *Sepala circa 1.25 mm. longa, vix 1 mm. lata, subdeltoidea, tenuiter acuminata, plus minusve inciso-dentata, roseo-tincta, interdum in fructu persistentia*. *Corolla minima, 3.5–4 mm. longa, rosea; petalo superiore alis roseis sursum curvatis grosse dentatis* carinam paulo superantibus apicemque attingentibus *obtusis*, atque calcare breviusculo rotundato; *petalo inferiore* marginibus angustis patulis apicem attingentibus *obtusis subspathulatis*; petalis interioribus apice sursum curvatis atropurpureis. *Fructus minimi, 1.5 mm. longi et saepissime paullulum latiores, subrotundi, superne rotundato-obtusi et inferne satis contracti, parum compressi sed modice carinati, in sicco apicis foveolis distinctis tenuiter rugosi*.

Omnium *Fumariarum* haec species in omnibus partibus minima est. Quamvis propter corollae formam *F. indicae* Pugsley maxime affinis sit, attamen per folia laciniis minimis angustissimis decomposita cum *F. parviflorâ* Lamk. (praesertim var. *glauca* Clav.) facilius confundi potest. Sed *F. parviflora* non solum planta omnino major robustiorque est sed etiam racemis vix paucifloris, bracteis brevioribus, pedicellorum apicibus minus incrassatis, sepalis relative minoribus, petali superioris alis subpatentibus raro dentatis, fructibusque majoribus minus rotundatis specificè differre videtur.

*F. minima* in declivis rupestribus Montis Carmel prope Haifam Palaestinae crescit, ubi a cl. Herr Bertschinger (anno 1935) collecta est.

This new species is an exceedingly pretty and dainty plant which has hitherto been overlooked, possibly owing to its likeness to a miniature *F. parviflora* var. *glauca*. But in spite of their diminutive size the specimens collected possess what appear to be fully developed flowers, and seem to be normal examples of a species essentially small in all its organs, which forms a very interesting addition to the flora of Palestine.

43. *FUMARIA VAILLANTII* Loiseleur.

The North African range of this species, hitherto known in its typical form only from Bedeau in the province of Oran, can now be considerably extended. There is a specimen in Herb. A. Faure from Ain-Sefra (Courzeille, 1904 !), near the Moroccan frontier; and examples, collected in 1933 and 1934, have been received through M. Emberger from two stations in the Grand Atlas Oriental (Anemzi and Ayachi). The plant thus ranges from south-western Algeria across south-eastern Morocco to the Central Grand Atlas and the Moyen Atlas, where it occurs as the distinct variety *maroccana* Pugsley.



46. *FUMARIA PARVIFLORA* Lamarck.

This was discovered by Duccellier in 1913 at the Oasis of Bilma, in the Soudanese Sahara—its extreme southern limit in Africa.

RUPICAPNOS.

SECTIO IV. CALLIANTHOS.

SUBSECTIO I. PERENNES.

To cover recently described species in this Subsection an addition should be made to its diagnosis, as shown in italics, thus :—‘*Plantae perennes, ± carnosae. Racemi multiflori, nisi in R. parvicalcaratâ et in R. rifanâ.*’

Series *Cerefoliae*.

Mr. C. S. Garnett collected in 1934 at Petitjean, in Morocco, a form somewhat resembling *R. graciliflora* Pomel, but distinguished by unusually long bracts and large, slender corollas with relatively short spurs. His specimens are unfortunately without fruit, but have the aspect of an undescribed species.

16 a. *RUPICAPNOS PARVICALCARATA*, sp. nov. (Pl. 24, fig. 1.)

*Exsicc.* Emberger, Amejjag, Mgouna (1,800–1,900 m.), 1933 (typus in Hb. Pugsley) !

*Rupicapnos perennis, relative nana, caudice crassiusculo ramoso decumbente et caulibus brevissimis praedita. Folia parva, pleraque radicalia, carnosae, verisimiliter vix glauca, 5–8 cm. longa (petiolo crassiusculo incluso), longissime petiolata, oblongo-deltaidea, foliolis 2–3-paribus subsessilibus vel infimis breviter petiolatis et segmentis secundariis in lacinias parvas oblongas subacutas irregulariter fissis 2–3-pinnatisecta. Racemi corymbiformes, sub-10-flori, cum pedunculo crassiusculo circa 10 mm. longo foliis plus duplo breviores. Bractee circa 1 mm. longae, ovatae, obtusissimae, subintegrae; pedicelli fructiferi graciles, apice vix dilatati, infimi ad 25 mm. longi. Sepala 1.5 mm. longa, 1 mm. lata, subrotundo-ovata, peltata, subacuta, inciso-dentata vel laciniata, albida. Corolla 13–14 mm. longa, haud gracilis, carinis viridibus albida; petalo superiore marginibus albidis apice valde dilatatis sursum reflexis carinamque longe superantibus obtuso, calcare circa 3 mm. longo angusto abrupte curvato deflexo; petalo inferiore marginibus albidis apice paulo dilatatis lineari subspathulato subacuto, basi leviter gibboso-saccato; petalis interioribus apice sursum curvatis plane alatis purpureis. Stylus malleiformis. Fructus mediocres, sine mucrone longiusculo circa 2.5 mm. longi, 2 mm. lati, subelliptici, obtusiusculi, valde mucronati, inferne multo angustati, parum compressi sed satis carinati, siccitate omnino dense tuberculato-rugosi.*

*R. parvicalcarata* per folia tenuiter dissecta ad Seriem *Cerefoliarum* Sectionis *Callianthos* plane pertinet, et in habitu, ut videtur, nano praesertim *R. ochraceae*

Pomel, *R. platycentrae* Pomel et *R. argenteae* Pugsl. subsimilis est. Ab duabus speciebus a Pomel descriptis, et ab hujus seriei aliis speciebus propter petali superioris calcar minimum valde differt. Hoc calcar non modo breve sed angustum et abrupte deflexum est. In *R. argentea* calcar, quamvis haud multo longius tamen rotundatum et vere multo majus fit. Petali superioris margines dilatati, qui carinam omnino occulunt, *R. parvicalcaratae* aliam notam propriam constituunt.

Haec species nova in rupibus calcareis Amejjag (1,800–1,900 m. alt.), prope Mgounam in declivitate australi Atlantis Majoris (Djebel Sagho vel Sairro) Mauritaniae crescit.

This is believed to be the first *Rupicapnos* collected on the south side of the Great Atlas of Morocco.

#### Series *Africanae*.

##### 17 a. *RUPICAPNOS SPLENDENS*, sp. nov. (Pl. 24, fig. 3.)

*Exsicc.* E. Wall, Sidi al Dallah, S.W. of Taza, 22. 5. 34 (typus in Hb. Pugsley) !

*Rupicapnos*, ut videtur, perennis, caudice crassiusculo ramoso decumbente caulibusque semper brevibus praedita. *Folia* plus minusve glauca, carnosa, ad 13 cm. longa (petiolo crassiusculo ad 6 cm. longo incluso), *oblongo-delloidea*, foliolis 2-(rarius 3-)paribus subdelloideis breviuscule petiolatis et segmentis secundariis *in lobos oblongos acutos* rarius submucronatos irregulariter fissis 2-3-pinnatisecta. *Racemi* corymbiformes, *multi*-(15-30)-*flori*, cum pedunculo satis crasso 4-5 cm. longo *foliis tertiâ parte breviores*. *Bracteae* circa 2 mm. longae, *ovatae*, *acutae* vel *acuminatae*, nonnunquam apicem versus *dentatae*; *pedicelli fructiferi graciles*, apice *incrassati*, *infimi ad 45 mm. longi*. *Sepala* circa 2.5 mm. longa, 1.5 mm. lata, *ovata*, *peltata*, *acuta*, *basi plus minusve laciniata*, albida. *Corolla maxima*, 15-18 mm. longa, vix *gracilis*, carinis viridiusculis albida; *petalo superiore* marginibus *purpureis* apice valde dilatatis sursum reflexis carinamque multo superantibus *obtusos*, *calcare* 5 mm. longo *recto apice rotundato*; *petalo inferiore* marginibus *purpurascens* apice dilatatis *lineari-subspathulato obtusos*, basi plane *gibboso-saccato*: *petalis interioribus* apice sursum curvatis *modice alatis atropurpureis*. *Stylus* malleiformis. *Fructûs magni*, sine mucrone 3-3.5 mm. longi, 2.75-3 mm. lati, *subrotundo-obovati*, *obtusiusculi*, *breviuscule mucronati*, inferne valde angustati, parum compressi sed plane carinati, siccitate omnino *grosse tuberculato-rugosi*.

Haec pulchra species, propter flores maximos notabilis, inter *R. speciosam* Pomel et *R. africanam* Pugsl. medium fere tenet, et ad Seriem *Africanarum* certe referenda est. *R. speciosa* foliis oblongis in lobos longiores fissis, corollis minoribus angustius alatis, fructibusque multo minoribus conspicue compressis satis differt. *R. africana* per folia minus dissecta, flores petalis exterioribus apice vix dilatatis minores, fructûsque ovatos longius mucronatos specificè

differre videtur. *R. Mairei* Pugsl. foliis anguste oblongis, floribus multo minoribus, fructibusque obovatis primo intuitu separatur. Propter folia deltoidea, flores minores pallidiores fructusque obtusiores magis rotundatos *R. decipiens* Pugsl. distinguenda est. *R. Faurei* Pugsl. et *R. rifana* Pugsl. habitu relative humili, foliis solum 2-pinnatisectis floribusque multo minoribus longe distant.

*R. splendens* rupes calcareas Sidi al Dallah prope Tazam Mauritaniae habitat, ubi a cl. Erik Wall inventa est.

This beautiful *Rupicapnos*, the finest-flowered of all the species at present known, is closely allied to *R. speciosa* and especially *R. africana* (sensu stricto). Its general resemblance to the latter, including the characters of the foliage and the fruit, might almost warrant its treatment as a variety of that species, but the much greater size of its flowers, with their different form and colouring, seems to justify its claim to independent specific rank.

19. *RUPICAPNOS AFRICANA* Pugsley in Journ. Linn. Soc., Bot., xlvii, 464 (1927), non Pomel.

Under the Rules of Nomenclature, as amended at Cambridge in 1930, homonyms are no longer admissible (Rule 61), and the above name thus becomes invalid. It is therefore proposed to substitute *Rupicapnos corymbosa*, based on *Fumaria corymbosa* Desfontaines in Act. Soc. Hist. Nat. Paris, i, 26 (1792), which is synonymous with *F. africana* Lamk. Encycl. ii, 569 (1788).

In the Revision (p. 345) a variety *mauritanica* of *R. decipiens* Pugsl. is described, for which two specimens collected at Tetuan are cited. Of these Hooker's is an adequate example, and it is from this plant that the description is taken. The other specimen, collected by Ball, is fragmentary, consisting only of two damaged leaves, two flowers, and no fruits. In the spring of 1935 a *Rupicapnos* was collected at Tetuan, close to the town, by Mr. C. S. Garnett, which differs from var. *mauritanica* in its more angular leaf-cutting, its less winged and more acute outer petals, and its more compressed and longer-mucronate fruits. These features bring it to *R. corymbosa*, but it is readily distinguishable from the typical form of this species by its more finely cut and deltoid foliage, distinctly pink-tinted flowers, and more compressed and carinate fruits, which recall those of *R. cerefolia* Pomel. On the whole, it seems to be related to *R. corymbosa* rather than *R. decipiens*, and it is therefore distinguished below as a variety of the former species. Ball's fragmentary specimen appears to match this form rather than the plant collected by Hooker.

*Rupicapnos corymbosa* (Desf.) Pugsl. var. *colorata*, var. nov. (Pl. 24, fig. 4.)

*Exsicc.* Garnett, Tetuan, 1935 (typus in Hb. Mus. Brit.) !

Planta foliis saepe subdeltoideis, sepalis leviter nec valde dentatis, corollis omnino roseo-tinctis, fructibusque subrotundo-obovatis satis compressis plane carinatis a typo differt.

Series *Pomellanae*.

Add to diagnosis of Series as shown in italics, thus :—

‘Folia . . . Flores pallide purpurei vel albid.’

22 a. *RUPICAPNOS AMBIGUA*, sp. nov.

*Exsicc.* Maire, Iter Marocc. xxvii, Immouzer, leg. G. Malençon, 1936 (typus in Hb. Pugsley) !

*Rupicapnos* perennis, glauca, caudice ramoso crassiusculo decumbente et caulibus brevissimis praedita. *Folia* pleraque radicalia, carnosa, glauca, 5–12 cm. longa (petiolo crassiusculo incluso), longe petiolata, *oblongo-delloidea*, foliolis infimis breviter petiolatis reliquis subsessilibus et segmentis secundariis subflabellatis *in lobos breviusculos rotundatos submucronulatos vel ovaes obtusos* saepe incisos irregulariter fissis 2-pinnatisecta, primaria simpliciora. *Racemi* corymbiformes, 10–20-flori, cum pedunculo brevi *foliis saepissime plus duplo breviores*. *Bractae* 1.5–2 mm. longae, *late ovaes*, acutae, apicem versus dentatae ; *pedicelli fructiferi graciles*, apice incrassati, flexuosi, infimi ad 35 mm. longi. *Sepala minima*, 1.5–2 mm. longa et paululum angustiora, ovato-rotundata, peltata, acuta, praesertim basin versus *inciso-dentata* vel laciniata, saepius roseo-tincta, facile caduca. *Corolla* 12–14 mm. longa, carinis viridibus *albida apice lilacino-tincta* ; *petalo superiore* marginibus apicem versus paulo dilatatis subpatentibus *oblongo obtuso*, *calcare circa 4 mm. longo* apice rotundato ; *petalo inferiore* marginibus latiusculis apicem versus sensim paululum dilatatis *lineari-oblongo obtusiusculo*, ad basin ipsam *obscure gibboso-saccato* ; *petalis interioribus* sursum curvatis *apice modice alatis a'ropurpureis*. Stylus malleiformis. *Fructus magni*, sine mucrone longo quadrangulato 3–3.5 mm. longi, 2.5–2.75 mm. lati, *oblongo-elliptici, subacuti, mucronati*, inferne valde angustati, satis compressi et plane carinati, siccitate omnino *dense tuberculato-rugosi*.

Haec species inter *R. speciosam* Pomel et *R. oranensem* Pugsl. medium fere tenet et in *Pomelianarum* Serie optime locanda est. Folia ut in *R. oranensi* lobis latis rotundatis conspicue crassa habet, sed fructus, quamquam minus compressos, eis *R. speciosae* simillimos.

*R. ambigua* in fissuris rupium calcarearum Atlantis Medii infra Imouzer Mauritaniae (1,100 m. alt.) crescit, ubi a cl. G. Malençon mense junio, 1936, collecta est.

This plant has been described from a single but adequate specimen, with good foliage, flowers, and fruits, kindly sent by Dr. Maire.

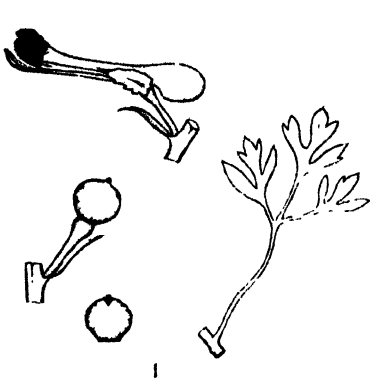
SUBSECTIO II. *ANNUAE*.

Insert in diagnosis of Subsection as italicised, thus :—

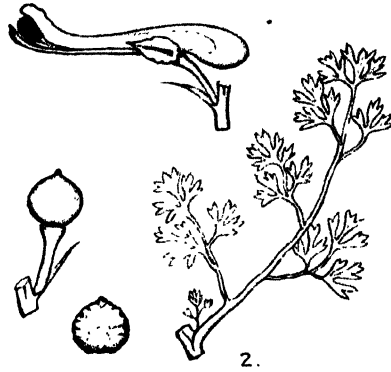
‘Plantae . . . Racemi saepissime pauciflori.’

23. *RUPICAPNOS GAETULA* (Maire) Pugsley. .

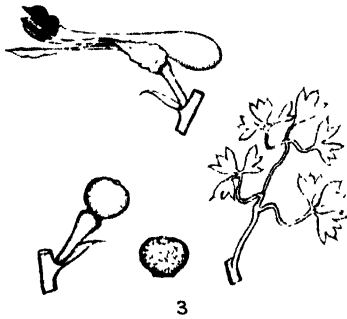
In 1935 Dr. Maire sent a specimen that must be referred to this species collected at El Guerouta, in the south of the province of Oran, by Dr. H. Foley.



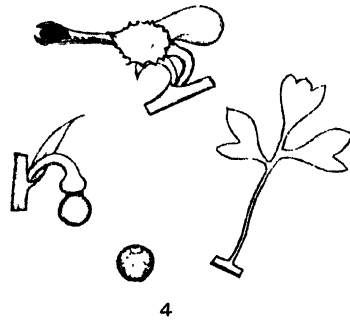
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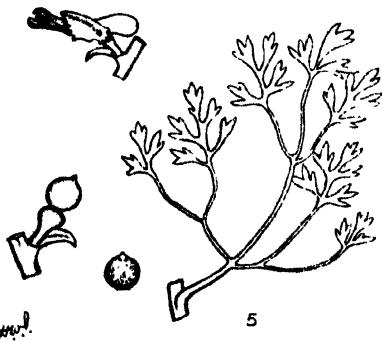
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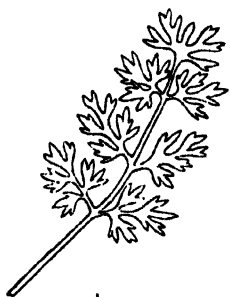
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Johnston & L. Johnston 194 London

1. *FUMARIA IFRANENSIS* PUGSL.  
2. *F. MICRANTHIFOLIA* PUGSL.  
3. *F. UNDULATA* PUGSL.

4. *F. MEKILLAICA* PUGSL.  
5. *F. OBTUSISEPALA* PUGSL.  
6. *F. MINIMA* PUGSL.

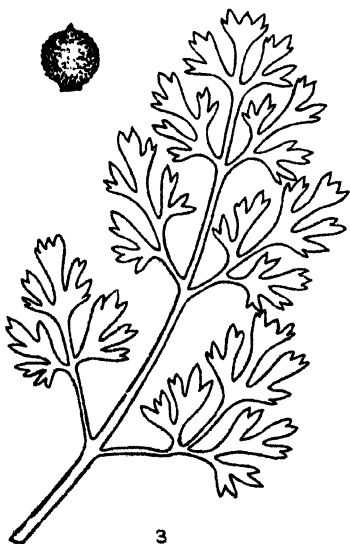
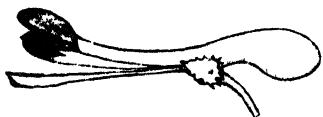




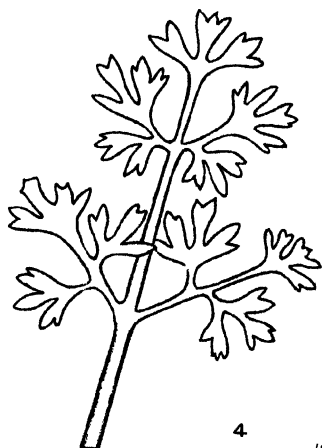
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H.W.P.

John Bale Sons & Tinnerman, 114 London

1. *RUPICAPNOS PARVICALCARATA*. PUGSL.
2. *R. ANOMALA* PUGSL.
3. *R. SPLENDENS* PUGSL.
4. *R. CORYMBOSA* VAR. *COLORATA* PUGSL.





This plant, a well-grown example, has floriferous racemes (up to 20-flowered) borne on peduncles over 3 cm. long, but corollas smaller than those of the type and not much exceeding 12 mm. in length.

24 a. *RUPICAPNOS ANOMALA*, sp. nov. (Pl. 24, fig. 2.)

*Exsicc.* Emberger, Près Anoccur, Moyen Atlas, 1934 (typus in Hb. Pugsley) !

*Rupicapnos annua*, radice longo, et caule crassiusculo ad 6 cm. longo, ut in speciebus perennibus nonnunquam decumbente et satis ramoso. *Folia* plus minusve carnosa et glauca, longissime petiolata, 6–20 cm. longa (petiolo gracili incluso), *oblongo-deltoides*, foliolis 2-paribus inferiore longe superiore breviuscule petiolatis, et segmentis secundariis in *lacinias oblongas mucronatas vel obtusiusculas* irregulariter fissis *2-pinnatisecta*. *Racemi* corymbiformes, *sub-12-flori*, cum pedunculo ad 25 mm. longo *foliis multoties breviores*. *Bractee* 1.5–2 mm. longae, *lanceolatae*, interdum apicem versus serrulatae, acuminatae; *pedicelli fructiferi filiformes* apice paulo incrassati, *infimi ad 25 mm. longi*. *Sepala* 1.5–2 mm. longa, 1–1.25 mm. lata, *lanceolato-deltoides*, vix peltata, longe acuminata, *basin versus argute dentata*, nervo dorsali viridiusculo albida. *Corolla* 9–11 mm. longa, *satis angusta*, ut videtur *albida lilacino-tincta*: *petalo superiore* marginibus apice paulo dilatatis plus minusve patentibus *anguste oblongo, subacuto, calcare* circa 3 mm. longo *leviter deflexo*; *petalo inferiore* marginibus apice vix dilatatis *lineari-oblongo subacuto*, basi *gibboso*; *petalis interioribus apice* sursum curvatis *satis dilatatis plane alatis atropurpureis*. *Stylus submalleiformis* lobis erecto-patentibus potiusquam divaricatis. *Fructus majusculi*, sine mucrone 2.5–2.75 mm. longi, 2–2.25 mm. lati, *obovati, obtusi, breviter mucronati*, inferne valde angustati, parum compressi et obscure carinati, siccitate omnino *dense tuberculato-rugosi*.

*R. anomala*, quarta species annua Sectionis *Callianthos* nunc inventa, per stylum haud vere malleiformem ut in hujus Sectionis aliis speciebus notabilis est. Propter corollae formam *R. fraternae* Pugsl. proxima est, car petalorum exteriorum margines paululum dilatati et petala interiora alâ dorsali bene explicatâ insolenter lata sunt, sed *R. fraterna* habitu nano foliisque normaliter trisectis satis differre videtur. *R. gaetula* (Maire) Pugsl. et *R. elegans* Pugsl. per flores multo majores longe distant.

Haec nova species in rupibus calcareis prope Anoccur in Atlante Medio Mauritaniae invenitur.

This is the only annual species hitherto seen in the Moyen Atlas of Morocco.

# EXPLANATION OF THE PLATES.

## PLATE 23.

Fig. 1. Leaflet of *Fumaria ifranensis* Pugsl., with flower and fresh and dried fruits.

Fig. 2. Leaf of *Fumaria micranthifolia* Pugsl., with flower and fresh and dried fruits.

Fig. 3. Leaf of *Fumaria undulata* Pugsl., with flower and fresh and dried fruits,

Fig. 4. Leaflet of *Fumaria melillaica* Pugsl., with flower and fresh and dried fruits.

Fig. 5. Leaf of *Fumaria obtusisepala* Pugsl., with flower and fresh and dried fruits.

Fig. 6. Shoot of *Fumaria minima* Pugsl., with flower and fresh and dried fruits.

Foliage all natural size ; flowers and fruits,  $\times 2.5$ .

PLATE 24.

Fig. 1. Leaf of *Rupicapnos parvicalcarata* Pugsl., with flower and dried fruit.

Fig. 2. Leaf of *Rupicapnos anomala* Pugsl., with flower and dried fruit.

Fig. 3. Leaf of *Rupicapnos splendens* Pugsl., with flower and dried fruit.

Fig. 4. Leaf of *Rupicapnos corymbosa* var. *colorata* Pugsl., with flower and dried fruit.

Foliage all natural size ; flowers and fruits,  $\times 2.5$ .

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